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# STUDIES

FROM THE

## MORPHOLOGICAL LABORATORY



UNIVERSITY OF CAMBRIDGE.

EDITED BY

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# A MONOGRAPH

OF

THE DEVELOPMENT

OF

# PERIPATUS CAPENSIS

BY

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## PREFACE.

THE present Monograph is, with the exception of slight additions and corrections, a reprint of a series of papers which appeared in the *Quarterly Journal of Microscopical Science* during the years 1885—8.

Owing to the rather long period over which the publication has extended, there is I fear a certain amount of repetition and of irregularity in the arrangement of the matter, for which I must apologise to the reader. I have attempted to reduce any confusion, which may be caused by the latter defect, by a detailed table of contents and by the series of diagrams on Pl. XIII., which will I hope show at a glance the method of development of the chief organs.

I may take this opportunity of stating that while my series of *Capensis* embryos is quite complete, there is a considerable period in the development of *P. Balfouri* of which I have but little or no knowledge. Between the stage of Fig. 12 Pl. I. and a stage resembling the *Capensis* embryo shown at Fig. 26 Pl. II., I have only one stage of *Balfouri* and that of a structure quite unlike anything in the development of the larger species. These embryos (Pl. I. Fig. 16), of which I have large numbers, appear to consist of a reticular mass of branched cells *completely* surrounded by a layer of flat cells. The existence of this stage seems to me to indicate that the development of *Balfouri* between the limits described above does not take the same course as in *Capensis* and that an examination of it would prove to be of considerable interest.

My series of *Balfouri* embryos is complete up to and after this period, and shows that the development does not differ essentially from that of *Capensis*.

When Balfour found the embryos of *Peripatus Capensis* with an elongated and divided blastopore, it seemed probable that the development would prove to be of more than usual interest. This has I think been thoroughly borne out by the investigation, the results of which are recorded in the following pages. The more striking features of the development are enumerated in the following statement:—

The large size of the egg combined with the almost total absence of yolk; the character of the cleavage; the structure of the gastrula, and the mode of origin of the enteron; the division and persistence of the blastopore as the mouth and anus; the position of the primitive streak behind the anus and its exact resemblance in structure to the primitive streak in Vertebrata; the presence of a pair of somites in front of the mouth (in the preoral lobes) sending prolongations into the antennæ and developing the rudiments of nephridia; the origin of the generative elements as nuclei in the endoderm which subsequently migrate into the mesoderm; the presence of the nephridial end-sacs, and the cœlomic nature of the generative tubes; the persistence of the cerebral grooves as the sub-cerebral bodies of the adult; the origin of the lining of the proctodæum and stomodæum from nuclei at the lips of the blastopore intermediate between the nuclei of the ectoderm and endoderm; and lastly the presence of a pale subcutaneous network from which the somatic muscles and nerves are probably developed in continuity with each other.

Of the morphological significance of these facts this is not the place to speak, but I may perhaps draw attention to two subjects of a general interest which are touched upon by my investigations.



The first of these relates to the continuity which exists at all periods of development between the protoplasm of adjacent cells—a continuity which is more marked in the segmenting ova and younger embryos than in the older embryos and adult. It would appear indeed that in *Peripatus* the cells of the adult, in so far as they are distinct and sharply marked off structures, are not, as appears to be generally the case, present in the earliest embryonic stages, but are gradually evolved as development proceeds. In other words the cell theory, if it implies that the adult cells are derived from embryonic cells, which have been directly produced by the division of the ovicell, does not apply to the embryos of *Peripatus*.

The second subject concerns the cœlom. This organ is more fully defined, and its condition in certain of the higher groups more clearly brought out than has hitherto been done.

Some of the figures on Pl. I. are not perhaps quite as clear as they should be. This is particularly the case with regard to Figs. 10, 11, 12, 13. These figures are all drawn from the ventral surface, i.e. from the surface opposite to the ectoderm patch, so that the latter (*ec.*) is in all of them supposed to be further removed from the observer than the endoderm mass (*en.*). To explain them still further I may add that Fig. 16 on Pl. IV. represents a transverse section through an embryo of the stage which these figures illustrate (near one side of the ectoderm patch). Further, Fig. 8 is viewed from the animal pole: the difference in level of the ectoderm patch (*ec.*) and the endoderm masses (*en.*) is not brought out in the lithograph. Fig. 10 on Pl. III. is a diagram illustrating a transverse section through this stage.

TRINITY COLLEGE, CAMBRIDGE.

9 August, 1888.

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DESCRIPTION OF PLATES.

## INTRODUCTION.

THE development of *Peripatus capensis* was first studied by Moseley,<sup>1</sup> who stopped for a short time at the Cape in November and December some years ago. His observations related only to stages which were comparatively late in development. Balfour, in 1882, found some younger embryos in specimens collected by Mr. Lloyd Morgan in July and August, and sent to Professor Huxley, who gave them to Balfour. He had only time to make a very few observations, of which he left a short record in the form of four rough drawings and a short note, and a letter to Professor Kleinenberg, before starting on his last expedition to Switzerland. His observations were so interesting that they were made the subject of a short communication to the Royal Society in the autumn of 1882, and they were slightly extended by the editors of his last work on the 'Anatomy of *Peripatus capensis*,' and published with that monograph in the 'Quarterly Journal of Microscopical Science' in the spring of 1883.

The subject seemed so important that the Government Grant Committee of the Royal Society granted, in the spring of 1883, the sum of £100 to enable me to go to the Cape for the purpose of obtaining well-preserved embryos, and of studying the development on fresh specimens.

Accordingly, I went to the Cape in the summer of 1883, arriving early in July, and remaining till the middle of August. I obtained a large number of specimens, and brought back with me over 300 alive. Some of the latter lived at Cambridge till the following July. The results of my observations at the Cape and after my return to England have been

<sup>1</sup> 'Phil. Trans.,' vol. 164.



to show that the embryos remain thirteen months in the uterus; that the fertilised ova pass into the uterus in April, and the young are born, fully developed, in the May of the year following. That is to say, the young ova pass into the uterus one month before the young of the previous year are born. I was not prepared for this, and I did not, in 1884, examine my specimens for the early stages until May, when the young were being born. The result was that I missed the early stages of development, and had it not been for the kindness of Mr. Walter Heape, who went to South Africa last summer, and who collected and brought back some more live specimens, I should have been obliged to leave the early stages undescribed. Thanks to him, however, and to my experience gained in the previous year, I was able, in 1885, to find several of the younger stages, and to complete my observations.

Two species of *Peripatus* are commonly found at the Cape. One, the most common, is the well-known *Capensis*; the other is a new species, differing from *Capensis* in having eighteen pairs of fully-developed legs, in being of a smaller size, and in other points. This species I propose to call *Peripatus Balfouri*. It will be fully described in the forthcoming monograph by Moseley and myself on the 'Species of *Peripatus*.'

Besides the work of Balfour and Moseley on the development of *Peripatus capensis*, some observations on the development of a West Indian species have been published by Dr. J. Kennel, of Würzburg.<sup>1</sup> The early stages, to which Dr. Kennel's observations mainly relate, are obviously extremely difficult to follow in the West Indian species, and I do not think that his account of them in the paper above referred to can be regarded as entirely satisfactory. There can be no doubt, however, that the early stages in the development of the West Indian species differ from those of the Cape species; for instance, there do not appear to be any structures in the Cape species which correspond to the amnion and placenta described by Dr. Kennel.

<sup>1</sup> Semper's 'Arbeiten,' Heft ii, Bd. 7.

Some of the more important results of my observations on the development of *Peripatus capensis*, e. g. the derivation of the mouth and anus from the blastopore, the fate of the grooves in the cerebral ganglia, have already, some time ago, been published in my paper<sup>1</sup> "On the Origin of Metameric Segmentation," and a preliminary account of them has been (May, 1885) communicated to the Royal Society.

All the drawings for Plates 1 and 2, with the exception of figs. 23—27, have been made by Mr. E. Wilson, of the Cambridge Scientific Instrument Company. They are very careful and accurate representations of the specimens, and I cannot sufficiently express my thanks to Mr. Wilson for the great trouble he has taken with them. The segmentation stages were all drawn in the laboratory as I removed them from the uterus, and the drawings<sup>2</sup> form a permanent and accurate record of the various stages of the living segmenting ovum.

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#### THE GENERATIVE ORGANS.

At the outset I must give a short description of the general arrangement of the generative organs. Their minute structure I shall describe more fully when I come to their development.

**Male Organs.**—The description given by Moseley<sup>3</sup> and by Balfour<sup>4</sup> is correct so far as the general arrangement is concerned, but a slight rectification is necessary in the significance to be attached to the various parts. The structures called testes by these authors (Balfour, loc. cit., Pl. XX, fig. 43, *te.*) are apparently merely seminal vesicles, in which the spermatozoa develop and gain maturity. The true testes are the so-called prostates (Balfour, loc. cit., fig. 43, *pr.*), the lining cells of which fall into the cavity of the tube, pass into the swollen seminal vesicle, where they develop into spermatozoa. The

<sup>1</sup> 'Quart. Jour. Mic. Sci.,' 1884.

<sup>2</sup> I regret to say that the lithographer has not done justice to the original drawings.

<sup>3</sup> 'Phil. Trans.,' vol. 164.

<sup>4</sup> 'Quart. Journ. Mic. Sci.,' 1883.

spermatozoa, when ripe or nearly ripe, pass into the vasa deferentia, at the lower end of which they apparently become packed together in small masses, which become surrounded by a structureless coat, and are passed out as small, oval, white spermatophores.

The male generative organs of *Peripatus capensis* consist, therefore, of a pair of blind tubes, which are separate in front, but united behind for a short distance to form a common terminal portion (Balfour, loc. cit., fig. 43, *p*), and at the front end of which are formed the mother-cells of the spermatozoa. The latter fall into the cavity of the tube, and gradually develop as they pass backwards towards the external orifice, the main portion of the development taking place in a specially dilated portion of the generative tube—a portion which may be called a vesicula seminalis.

I have never seen the extrusion of the common terminal portion of the system, and I doubt very much whether it ever is extruded so as to act as a penis.

**The Female Organs.**—The ovary, though apparently a single structure, is in reality paired, and consists of two tubes closely applied together. The ova are derivatives of the epithelial lining of these tubes. Each ovarian tube is continued into the oviduct of its own side. The oviducts are united with one another close to the ovaries; they are thin-walled, narrow tubes, each of which is continued behind into a more dilated and thicker-walled tube—the uterus. The uterus is of considerable length and much bent, and unites with its fellow close to the single external opening, which lies in the middle line of the ventral surface of the hind end of the body, just in front of the anus. For figure of female organs, *vide* Moseley, loc. cit., pl. 74, fig. 1, and Balfour, Pl. XIX, fig. 33.

From the above description it is evident that the organs of the female, like those of the male, consist of two tubes united behind near the external opening but ending blindly in front, where the generative products are produced.

The ovarian parts of the generative tubes are placed between the fifteenth and sixteenth pairs of legs, and are united to the



floor of the pericardium by a delicate band of transparent tissue. They, i. e. the ovaries, contain spermatozoa, some of which project through the ovarian walls into the body-cavity. This condition has been figured and described by Moseley (loc. cit., pl. 74, fig. 1).

The ovaries always contain spermatozoa, but in smaller numbers directly after the eggs have passed into the oviduct than at any other time. This is a very marked feature of an ovary, say, of the beginning of April, when compared with an ovary from which the ova have just passed into the oviducts, say, of the beginning of May, the former being of an opaque-white colour to the naked eye, while the latter has a much more transparent appearance.

This fact would seem to imply that fresh spermatozoa pass each year into the ovaries. This brings me to the question of the manner in which the male discharges his function. The vesiculæ seminales (testes of Moseley and Balfour) are almost empty of spermatozoa in the months of February, March, and April. At the end of April, however, they begin to swell again and contain spermatozoa, which increase in number as time goes on, until, in October, they are fully distended with spermatozoa in all stages of development. There seems to be no functional intromittent organ, but the male deposits little oval spermatophors quite casually on any part of the body of the female, and, for all that I know, of the male also; e. g. I have often seen them on the head. How these little packets of spermatozoa get into the vagina, and then up the uteri, which are always full of embryos, I cannot conceive. The spermatozoa exhibit a certain amount of vibratory movement, and no doubt, once within the vagina, they are set free from the spermatophor and make their way up the female generative tube, between the embryos and the uterine walls. Inasmuch as the deposition of spermatophors lasts from June until January, each female probably has a large number of spermatophors deposited on her, and some of these are probably near the generative opening, and are, somehow or another transported through it into the vagina.

Fertilisation is apparently effected in the ovary. I have never seen spermatozoa in any part of the female apparatus except in the ovaries, and in small numbers in the upper end of the oviducts at the time when the ova are entering the latter.

The ripe, and probably fertilised, ova pass into the oviduct in April, while the uterus is still full of embryos almost ready for birth. Segmentation and the early stages of development take place during the passage of the ova down the oviduct. In May the young of the previous year are born. Into the uterus, thus emptied, the young ova pass, and establish themselves in the positions which they maintain until the following May, when they are born.

The passage of the ova down the oviducts and <sup>1</sup> uteri is effected by the peristaltic contraction of the walls of these structures. I have never been able to see cilia in the generative organs, or in any other part of the body of *Peripatus capensis*.<sup>2</sup>

The living ripe ovarian ovum is somewhat elliptical in shape and of dark colour by transmitted light. The opacity is due to the presence of granules, which are uniformly distributed in the protoplasm, but absent altogether from the large germinal vesicle.

As I have stated above, I propose to defer my account of the ovary and ovarian ovum until their development is considered.

<sup>1</sup> The ovarian walls themselves contain muscles and are contractile.

<sup>2</sup> This remark applies to the nephridia, all parts of which I have carefully examined in the fresh state without ever seeing a trace of cilia.

## CHAPTER I.

### THE GENERAL DEVELOPMENT OF THE EMBRYO.

**The Fertilised Ovum.**—The youngest ovum found in the oviduct is shown on Pl. I, fig. 1. It is of an elongated form—length<sup>1</sup> .4 mm.—and is surrounded by a transparent, structureless membrane, within which is a second, more delicate membrane. The outer membrane persists until birth; it has a dense structure and allows fluid to pass through it by diffusion. Water diffuses through it more rapidly than alcohol, and alcohol more rapidly than turpentine; so that when an embryo is removed suddenly from weak alcohol into strong, or from absolute alcohol into turpentine, the membrane shrinks and closely invests the embryo; in fact, in the latter case all the alcohol diffuses out before any turpentine enters, so that the membrane completely collapses and squashes the embryo flat. When, on the other hand, an embryo is removed from strong alcohol into weak, or into water, the water passes in more rapidly than the alcohol passes out, so that the membrane is distended, and the space between it and the embryo much enlarged. In the normal embryos there always is a space between the membrane and the ovum, which contains fluid in which the embryo floats. The membrane, therefore, has much the same function as the amnion of the Vertebrata.

The protoplasm of the ovum<sup>2</sup> is differentiated into two parts—the main mass being of a pale colour with relatively few dark granules, while at one point it is especially dark in colour. This small dark patch (fig. 1) is placed at the surface on one of the

<sup>1</sup> This refers to *P. Balfouri*; in *P. capensis* the average length is .56 mm.

<sup>2</sup> The following description of the segmenting ova refers, unless otherwise stated, to fresh living ova seen in transmitted light.



long sides of the ovum. I may call it, from its position as determined by the later development, the dorsal or animal pole of the ovum. When the ovum is viewed from the side (fig. 1), it is seen that the surface of the dark patch is pitted inwards, and that the space so formed contains two small clear bodies, which I take to be polar bodies. When viewed from the face, the dark patch presents a central circular transparency more or less free from the dark granules which are found in such large numbers in other parts of it. This central clear body I take to be the first segmentation nucleus. The polar bodies are only seen on surface view during this stage, and I have no observation on their fate.

I have figured two other unsegmented ova (figs. 2 and 3) which differ in certain respects from the above. In one of these (fig. 2) the dark patch is smaller than in fig. 1, and without the central transparent area; in the other (fig. 3) there were several dark patches, each with its own clear spot.

#### GENERAL FEATURES OF SEGMENTATION.

The segmentation is apparently complete; i. e. the whole ovum appears to break up into separate cells. But as a matter of fact this is not the case; the so-called segments do not, as will be shown in the next chapter, completely separate from one another. For the sake of convenience, however, the terms "segmentation" and "furrow" will be employed in the present general account.

The first furrow is in the transverse plane of the ovum, and divides it into two halves (fig. 4), the dark patch being divided as well as the main mass of the ovum. The second furrow is at right angles to the first, and divides each of the first formed segments into two (figs. 5 and 6), so that the ovum now consists of four segments, each consisting of a lighter-coloured main mass and a small dark patch which closely adjoins the dark patches of the three other cells at the animal pole, and which contains a central clear area (fig. 5).

The two first furrows, therefore, are at right angles to one another, and in the vertical plane. The next furrow is also

vertical and parallel to the first furrow; it divides each of the four segments into two parts (fig. 7). Meanwhile the larger, clearer masses of the opposite side of the ovum are gradually separating from the darker cells of the animal pole, and breaking up into smaller masses of various sizes and irregular shape; they will henceforth be called the endoderm masses or cells, inasmuch as they give rise to the greater part of the endoderm. The small, darker cells, each of which contains a central clear area—the nucleus, give rise to and will be called the ectoderm.

Each of the ectoderm cells, which are apparently eight in number and arranged in two rows (four in each row), now divides along a line parallel to the long axis of the ovum, so that there are sixteen ectoderm cells arranged in four rows with four cells in each row.

The ectoderm cells continue to divide in this manner, and the endoderm masses become more broken up, until at the end of segmentation (fig. 8) the ovum consists of a number of large and small branched endoderm masses scattered irregularly within the egg membrane, while the ectoderm cells consist of a mosaic of more or less hexagonal cells closely applied together and placed close to the membrane on one side at about the middle of the long axis of the egg.

The egg at this stage presents a very peculiar appearance, and I would not believe for some time that I was not dealing with an abnormal or injured ovum. But I found the stage so often, and so many stages intermediate between it and the earlier and later stages of development, that I cannot but believe in its normal existence. I found it also when every precaution was taken to avoid injuring the ovum; when I merely opened the animal and examined the ovum through the transparent walls of the oviduct without even touching any part of the female organs.

The endoderm masses at this stage—and I have no doubt this is the case in other stages, but in this case the fact can be clearly seen—are branched, and the branches of adjoining masses in some cases anastomose. One must sup-

pose in fact that the endoderm cells of this stage are amœboid and capable of independent movement, in order to account for the changes which now take place.

In fig. 9 I have had drawn an embryo of this stage as an opaque object, with reflected light. The drawing shows clearly the mosaic of ectoderm cells, which in this light seem to be composed of a brilliant white substance with a central dark area.

The endoderm cells now begin to draw together towards the centre of the egg, and come to lie directly beneath the ectoderm mosaic, which rests upon them like a cap. I have had various stages of this process drawn in figs. 10—14.

This change can only be explained as being due to an active movement of the endoderm cells, which travel from all parts of the egg towards the centre, where they aggregate in masses which gradually unite with one another, forming at first a ring and then uniting further until they form one more or less spherical, and apparently, solid mass of cells on which the ectoderm mosaic rests like a cap. Fig. 15 shows a side view of an embryo at this stage, in which this process of aggregation of the endoderm cells is completed. Fig. 15 is drawn from a preserved embryo made transparent by turpentine.

The nucleus of the ectoderm cells, which has been conspicuous in all these stages by its transparency and freedom from granulations, presents quite a different appearance in embryos which have been treated with reagents. In the latter case instead of a central transparency, we find a central mass of dark granules, which are much more marked than the granules of the body of the cell. Further, it should be pointed out that, in the latter stages, the granulation of the ectoderm cells is a much less marked feature (*vide* figures), and that the boundary between the ectoderm cells becomes less distinct (*vide* especially fig. 13).

The ectoderm now grows round the endoderm cells and entirely surrounds them, excepting at one point. At this point, which is opposite to that on which the ectoderm cap



was placed, the endoderm cells may be seen for a short time projecting (figs. 17 and 18).

The embryo has thus acquired a spherical form, and consists of a solid gastrula, the small uncovered spot of endoderm constituting the blastopore. A cavity next appears in the centre of the endoderm cells, so as to open to the exterior through the blastopore (figs. 19 and 21).

We have thus arrived at the stage of a typical gastrula formed of two layers of cells, which are continuous with one another at the blastopore and enclose a central cavity. It may be at once stated that the blastopore, which is on the ventral surface of the embryo—on the surface opposite to that on which the ectoderm cap was placed—persists and gives rise to the mouth and anus<sup>1</sup> of the adult, and that the cavity of the gastrula becomes the mesenteron.

#### THE GENERAL FEATURES OF THE EMBRYO AT SUCCESSIVE STAGES.

The segmentation is then apparently complete but unequal; the large cells giving rise to the endoderm, and the small cells to the ectoderm. The gastrula arises by a modified process of epibole. The fully-developed gastrula is shown in figs. 19 and 21. The embryo has already become slightly oval, and the blastopore now begins to elongate in the direction of the long axis.

**Stage A (fig. 22).**—An opacity appears at the hind end of the blastopore. This opacity is the primitive streak. It appears to be due to the active proliferation of some cells, which cannot be definitely assigned either to the ectoderm or the endoderm, at the hind end of the blastopore. This stage, which has

<sup>1</sup> These were called in Balfour's memoir ('Q. J. M. S.,' 1883), and perhaps more correctly, the embryonic mouth and anus,—more correctly because they come in the adult to lie internally, in consequence of the ingrowth of ectoderm at the two ends of the alimentary canal to form the stomodæum and proctodæum. They constitute in the adult the openings between the mesenteron and the stomodæum and proctodæum respectively. It must, however, be borne in mind that they never become closed.

already been described in Balfour's Memoir on *Peripatus* (loc. cit.), is found most commonly at about the middle or June in England.

The embryo now grows considerably in length (fig. 23), the blastopore presenting a corresponding elongation, and the mesoderm, which arises from the proliferation of the undifferentiated cells of the primitive streak, grows forward as two ventrolateral bands, one on each side of the blastopore.

The mesodermal bands next divide by transverse division from before backwards into somites, each of which contains a cavity, part of the future body cavity. The first somite to appear is the anterior, and then successively backwards.

**Stage B** (fig. 25).—The blastopore now divides into two parts (figs. 24 and 25) by the obliteration of its median portion—into an anterior part which becomes the mouth of the adult, and a posterior part which is at first placed at some little distance from the hind end of the embryo and gives rise to the anus of the adult.

The primitive streak still persists and extends from the hind end of the blastopore to the hind end of the embryo. It is now marked by a groove—the primitive groove (fig. 25).

The anterior pair of somites have shifted forward to quite the anterior end of the body; they give rise to the mesoderm and body cavity of the præoral lobes.

**Stage C** (figs. 26 and 27).—The hind end of the body now becomes curved ventrally (figs. 26 and 27). The curve is produced by the growth of the hind end of the body. As this growth proceeds the curve becomes more marked, and assumes a spiral form, that is to say, the hind end of the body is spirally coiled, the coil being applied to the ventral face of the anterior part of the body (fig. 28).

Stages B and C are found in July and August at the Cape.

**Stage D** (figs. 28 and 29).—The spiral stage is characterised by the appearance of the appendages and of the lip-fold which encloses the jaws in the adult, and of the eyes.

The appendages arise as hollow processes of the body wall, containing prolongations of the somites. The first to appear are the antennæ, into which the præoral somites are prolonged. The remainder appear from before backwards in regular order, viz. jaws, oral papillæ, legs, 1, 2, . . . 17, and the rudimentary anal papillæ, which are the appendages of the last, i. e. the twenty-first somite.

The full number of somites and their appendages is not, however, completed until a later stage, the posterior being the latest to appear.

The eyes appear in this stage as invaginations of the sides of the nervous thickenings (the future supracæsophageal ganglia) of the præoral lobes (fig. 29, *e*). The invaginations are at first shallow, but soon become deeper, and in the next stage converted into closed vesicles, the front wall of which (i. e. the wall next the skin) forms the epithelium outside the so-called lens of the adult eye, while the internal wall thickens, and remains continuous with the cerebral ganglion, and gives rise to the retina. The enclosed vesicle persists, and apparently becomes filled by the structureless lens of the adult eye, if the structure described as such be not a mere coagulum produced by reagents. The eye of *Peripatus* is therefore a cerebral eye.

The lips.—The end of the spiral stage is also characterised by the appearance of the buccal fold or fold which encloses the jaws and buccal cavity, and so constitutes the tumid lips of the adult. This is a fold of the side walls of the body immediately outside the jaws, and extending from the præoral lobe of its side to just behind the jaw. It is at first most marked in front, which fact led Moseley to describe it as a backward process of the præoral lobe.

The first indication of the lip is shown in fig. 29, just behind the eye; it is seen better, however, in the figure of the next stage (fig. 30, *L*).

This stage is also characterised by the fact that the anus has shifted to the hind end of the body (the primitive streak having apparently disappeared), The præoral lobes have also



become markedly bilobed as compared with the previous stage (fig. 26).

Stage E (figs. 30—34).—In the next stage (fig. 31), which is found at the end of September and early in October in England, the spiral straightens out, and the embryo becomes bent double, the ventral surface of the hind part of the body being applied to the ventral surface of the front portion, and the tail end of the embryo being curled round the front end of the head. The bend occurs at the level of the eighth somite.

An embryo straightened out and drawn from the side is shown in fig. 30.

The main features of this stage, in addition to the loss of the spiral form, are—(1) the increase in the number and size of the somites and appendages; (2) the closure of the eye-pits; (3) the growth of the lips; (4) the appearance of a groove in the thickened ectoderm on the ventral surface of the præoral lobes; (5) the presence of a well-marked dorsal projection at the level of the anterior bend of the body; (6) the beginning of the ectodermal invagination which will form the stomodæum; (7) the appearance of a pit at the apex of the oral papillæ (fig. 33, *or. p.*); and (8) of a perforation on the hinder part of the ventral swellings at the base of the oral papillæ (fig. 33, *o. s.*).

With regard to these points, I may make the following observations:

1. The antennæ have become ringed, and the number of somites is almost completed. There are ultimately twenty-one somites; in this specimen twenty could be made out (fig. 32).

2. In the specimen figured (fig. 30) the eye-pits were not closed; they remained open in this specimen abnormally late.

3. The lip-fold has grown considerably, and extended on to the ventral surface behind the jaws (figs. 30, 33, *L.*).

4. These grooves are shown in fig. 35 (*c. g.*), which is taken from a young specimen of the next stage. They are at first wide and shallow, but, as we shall see, soon become deep and narrow, and eventually closed.

5. This projection had already appeared in the spiral stage (figs. 28, 29), but it first becomes conspicuous in this stage

(fig. 30, *d.*). It is placed at the level of the eighth somite, and consists simply of a thickening of the dorsal and lateral ectoderm.

6. This process is shown in its two first stages in figs. 33 and 34, *st.* In fig. 33 the posterior margins of the buccal opening are beginning to grow in beneath the anterior margins; the same feature being shown more clearly in fig. 34, *st.*

7. These pits are caused by an ectodermal invagination which will give rise to the slime glands.

8. These two perforations (fig. 33, *o. s.*) are actual perforations leading through the body wall into the body cavity of the third somite (somite of the oral papillæ); they become the external openings of the salivary glands.

Stage F (fig. 36).—The next stage, which is also found in October in England, is very close to the previous one, and I have only thought it necessary to figure a ventral view of the head (figs. 35, 36). Fig. 35 is from a specimen slightly younger than fig. 36, in fact from a specimen intermediate between this stage and the previous stage. It has already been referred to as showing the grooves in the brain (*c. g.*), which first appear in stage E. The main features of interest in this stage relate to the head and anterior somites.

(1) The lips have become very conspicuous and folded (fig. 36); they have extended on to the ventral surface, passing inwards between the jaws and oral papillæ, behind the openings of the salivary glands, which they have completely covered up, and finally have united with one another in the median ventral line, so as to form the posterior part of the adult lips.

Fig. 35 is especially interesting as showing an earlier phase in this growth. In this figure the folds have not yet reached the middle line, and are still very inconspicuous behind the salivary openings (*o. s.*), which are still exposed.

(2) The cerebral grooves (fig. 36) have become much deeper, and their opening reduced to a narrow slit, ending behind in the mouth and slightly dilated in front.

(3) The ingrowth of ectoderm into the mouth-opening is nearly completed in fig. 35. In fig. 36 the mouth-opening has

become much reduced by the approximation of the ventral swellings at the base of the jaws (cf. figs. 35 and 36, *j. s.*).

(4) The præoral or cerebral lobes, which were distinctly bilobed and separate in the previous stage (fig. 33), have now again become quite continuous across the middle line (cf. figs. 33, 35, 36), a shallow groove only marking the original line of separation.

**Stage G** (figs. 37, 38).—The last stage which I have thought it necessary to figure and describe is found in England in December (figs. 37, 38). The differences between this and the previous stage consist mainly in the growth of parts already present.

The embryo is characterised by its great transparency. The full number of appendages is present, and the appendages have acquired more nearly their adult form. They are all ringed, and the rudiments of claws have appeared on the legs. The appendages (fig. 37) are antennæ, jaws (now completely hidden by the lips) oral papillæ, seventeen pairs of legs, and the small anal papillæ (*an. p.*).

The skin presents slight projections, shown as white opaque marks in the figure; these are the commencement of the papillæ, which cover the skin of the adult. The dorsal projection is still a conspicuous object (*d*), though not so conspicuous as in the earlier stages.

The integument presents a ringed appearance (fig. 38); the rings, however, have nothing to do with the segmentation of the body, being far more numerous than the segments.

The mesenteron is distinctly visible as a wide tube which behind passes into the narrow rectum (*R*). The rectum is probably lined by an ingrowth of ectoderm through the anus and may be looked upon as a proctodæum.

The salivary glands (*s. g.*) can be seen through the skin, and have grown some distance backwards. The same is to be said of the slime glands (*sl. g.*) which, however, are directed more dorsally. The salivary glands are, as I have said in my preliminary paper, the nephridia of the third somite, i. e. the somite of the oral papillæ.



The remaining nephridia are also visible through the skin, those of the fourth and fifth legs being especially conspicuous by their greater size.

Fig. 38 represents this embryo in its natural position within the uterus, a position which is retained until birth.

From January onwards the changes are mainly those of growth. When the young are born, i. e. in May, the antennæ are green, but the rest of the body is either quite white or of a reddish colour. This red colour differs, however, essentially from that of the adult, in the fact that it is soluble in spirit. The just born young vary considerably in size, the average size in the case of *Peripatus capensis* being from 10—15 mm. The just born young of *Peripatus Balfouri* are about half this size.

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## CHAPTER II.

### THE SEGMENTATION OF THE OVUM AND FORMATION OF THE LAYERS.

THE ovum is composed of a spongework (Pl. IV, fig. 13), the strands of which consist of an apparently hyaline and structureless material and contain a small number of highly refractile globules of various, but always small, size. Globules of a similar nature are also found in the spaces of the spongework.

In the ovum of *Peripatus Balfouri*, and to a much smaller extent in the ovum of *P. capensis*, a number of angular bodies, staining slightly deeper than the rest of the reticulum, and in unstained specimens having a somewhat yellow tint, are present (Pl. IV, fig. 19, *s.b.*). At first I took these structures for a kind of yolk material contained in the meshes of the spongework, but a more careful examination has led me to believe that they are merely nodal expansions of the latter; they undoubtedly present the appearance of being continued at their angles into the strands of the reticulum (Pl. III, fig. 1, *s.b.*). The property which they possess of staining more deeply than the rest of the reticulum—a property which is only visible in sections through the ovum—is probably merely apparent and due to the fact of their greater mass.

There is then no yolk material in the ovum, unless these bodies and the small highly refractile globules which are present in very small numbers are to be regarded as such.

The sponge-like structure of the ovum of *P. capensis* is very conspicuous. The meshes of the spongework must be occupied

in life by a structureless fluid, for they contain in preserved specimens nothing presenting any structure, excepting the small number of globules and granules already mentioned. It can hardly be doubted, when the large size of the egg is considered, that some not very remote ancestors of the Cape species must have possessed an ovum, heavily charged with food yolk. We may further conclude from what we know of the relationship of the food yolk to the protoplasmic reticulum in other eggs, that this yolk must have been contained in the meshes of the reticulum, which now contain only fluid. This view is strongly confirmed by the fact that in a species of *Peripatus*, living at the present day and closely resembling *Capensis*, viz. *P. novæ zealandiæ*, the ovum is considerably larger than that of *Capensis* ( $1.5 \times 1$  mm.), and contains a large amount of food yolk. Our knowledge of the structure and early development of the ovum of this species is very small. It has been described by Hutton (6) and Kennel (8), and I have cursorily examined ova removed from hardened specimens. But the latter were too ill preserved to enable me to arrive at any satisfactory conclusions as to their structure and early development. There can, however, be no doubt on the following points:—(1) They are very large, (2) they have a thick chitinous shell, and (3) they are very heavily charged with food yolk. The shell of the Cape species, is as already stated, a somewhat delicate, transparent, structureless, but dense membrane; and within it, and much more closely applied to the ovum, there is a second, apparently similar, but more delicate membrane.

It is interesting to notice here the small size ( $.04$  mm.) of the ovum of the West Indian species as described by Kennel. The eggs of these three species seem to form a perfect series in regard to size<sup>1</sup> and amount of yolk, and it would be extremely interesting to compare their structure and the early stage of

<sup>1</sup> Greatest length of ovum of *P. novæ zealandiæ*,  $1.5$  mm.; of *P. capensis*,  $.5$ — $.6$  mm.; of *P. Balfouri*,  $.4$ — $.5$  mm.; of *P. Edwardsii*,  $.04$  mm. All the known species of *Peripatus* are viviparous and bring forth fully developed young.



their development. I regret, however, that the materials for this comparison are to a great extent wanting; for, although we know more of the development of the West Indian species than of the New Zealand one, thanks to the researches of Kennel, still, as I have pointed out (Chapter I, p. 2), the latter are too incomplete to permit of any profitable comparison.

After this account of the general structure of the ovum of the Cape species, I will describe the special features of the unsegmented uterine ovum at its different stages.

The unsegmented ova, which I have found, seem to belong to two distinct stages, each of which presents special features. There are (1) the stages before the conjugation of the male and female pronuclei; (2) the stages after that event.

1. The ova of this stage all belong to *P. Balfouri*; they are distinguished externally by the small size of the dark area in the living ovum (*vide* Chapter I, Pl. I, fig. 2), and by the apparent absence, in surface views, of the polar bodies. All of them, at least all those of which I succeeded in preparing good sections, presented indications, more or less distinct, of a male pronucleus, and in all polar bodies were being formed.

The ovum contained an irregular central cavity which, however, was not so well marked as in later ova. The reticulum was slightly denser round the nucleus than elsewhere. This slight increase in density is the cause of the small opaque spot in the fresh ovum. The nucleus was placed in the middle of the long axis of the ovum near the surface, and presented a different structure in every ovum of this stage which I examined. In all, except one which I have figured (Pl. III, fig. 1), it appeared to be undergoing changes in connection with the formation of the two polar bodies. I have four ova of this stage, and they all presented structures which I take to be the male pronucleus.

The polar bodies are two in number; when fully formed they have a diameter of about  $\cdot 016$  mm. Each of them contains a small number of deeply-staining bodies which are placed close together in the centre and represent the nucleus (Pl.

III, fig. 1). I have never seen an ordinary vesicular nucleus in a polar body.

The male pronucleus varied in the different ova. It was always placed near the surface almost opposite the female nucleus.

2. The ovum in which the male and female pronuclei had united<sup>1</sup> all presented essentially the same features so far as the body of the ovum was concerned, but differed in the structure of their nuclei. The structure of the ovum will readily be understood after an examination of fig. 8, Pl. III. There is a well-marked cavity traversed by irregular strands of protoplasm. The network is much closer round the nucleus than elsewhere. This feature of the perinuclear protoplasm is much more marked than in the earlier ova, and causes the large opacity noticeable in surface views of the ova of this stage (Pl. I, fig. 1).

The polar bodies present no essential differences from those of the previous stage. They persist during the early stages of segmentation.

The nucleus presented different appearances in the different specimens. In all, however, it was distinguished by its large sizes, and it seems to be the cause of the central transparency of the dark patch seen in fresh ova. Its structure will be described below.

#### THE SEGMENTATION.

The general features of the segmentation have already been described in the first chapter.

The first furrow passes through the centre of the opaque patch, and at right angles to the long axis of the ovum. Each of the two segments resulting from this consists of a small

<sup>1</sup> I have not observed the conjugation of these nuclei. I assume its occurrence from the analogy of other animals. In any case the ova I am about to describe were undoubtedly older than the preceding, and the nucleus is the first segmentation nucleus.

opaque portion, which contains the nucleus and is closely applied to the opaque part of the other segments (Pl. I, fig. 4). A careful examination of this ovum shows that the furrow has not completely separated the two segments from each other, but that they are connected by strands of protoplasm forming a loose network between them. This network is simply a looser part of the ordinary protoplasmic network described at the beginning of this chapter. There are, however, no such strands between the most superficial parts of the opaque areas; in this region the furrow is for the moment complete. Soon, however, the clearer protoplasm (where the network is looser and continued into the still looser network between the two segments) extends upwards on the inside of the dark patch, so that when four segments are formed by the second vertical furrow each dark patch is surrounded on all sides by a layer of the looser reticulum (Pl. I, fig. 5), which is here as elsewhere continuous with the reticulum of the adjoining segments.

Two changes now occur: (1) the pale, clearer, and larger part of the four segments begins to break up into smaller, irregular masses of varying size, which, however, are seen on careful examination to be connected with each other by a wide-meshed reticulum, and (2) a third furrow appears dividing the four dark patches, which I have called the ectoderm cells, into eight patches or cells (Pl. I, fig. 7). This furrow may be looked upon as corresponding to the horizontal furrow, which ordinarily follows the second vertical furrow in the segmentation of the ovum. The ovum therefore now consists of eight ectoderm cells, and four large and a number of smaller endoderm masses, all connected together by a wide-meshed reticulum, and placed immediately beneath the egg-shell around a central cavity—the segmentation cavity. Each ectoderm cell presents in the fresh specimen (Pl. I, fig. 7) (1) a central clear area—the expression of the nucleus; (2) around this a dark area—the expression of the dense protoplasmic reticulum around the nucleus; and (3) a paler circumferential area, which is more marked on the outer than on the inner border of the



cells. This is the expression of the looser part of the reticulum, which is continuous internally with the reticulum of the adjoining cells, and externally with the clearer masses constituting the rest of the ovum, and called by me the endoderm masses (Pl. IV, fig. 19). All the above elements are arranged round the central cavity, which was present even in the unsegmented ovum. Fig. 14, Pl. IV, is a diagrammatic representation of a transverse section through the ectoderm cells at this stage; it shows the continuity of the looser circumferential parts of the reticulum of the two cells (the endoderm masses are not represented in this figure).

The next divisions take place parallel to the long axis of the ovum, and result in the formation of sixteen ectoderm cells arranged in four rows, each row containing four cells. A diagrammatic transverse section of such an ovum is shown in fig. 15, Pl. IV, in which the endoderm masses are represented. This section also shows the segmentation cavity around which the various elements are arranged.

The further changes which may be considered as belonging to the segmentation stages consist in the continued and regular subdivision of the ectoderm cells, and in the continued breaking up of the endoderm masses into smaller bodies. Fig. 8, Pl. I, represents a fully segmented ovum. It consists of a small patch of ectoderm cells, and a number of irregular branched endoderm masses. Both the ectoderm cells and endoderm masses are placed immediately beneath the egg-membrane round the segmentation cavity. A diagrammatic representation of a transverse section of such an ovum is shown in Pl. III, fig. 10, and Pl. IV, fig. 17 is a drawing of an actual section through such an ovum in situ in the uterus.

The reticulum which connects the endoderm masses is shown—highly magnified—in fig. 7, Pl. III. It lies immediately beneath the egg-shell and consists of pale, hyaline strands, which at the nodes spread out into flat expansions. The strands contain a small number of strongly refractile globular bodies. This drawing was made from an uninjured ovum preserved in sublimate and acetic acid. The reticulum connecting the

ectoderm cells is shown in Pl. IV, fig. 12, made from an ovum of the same age and prepared in the same way as the last. This drawing represents one corner of the ectoderm patch; three whole cells and parts of three others are represented, and they are all seen to be connected by a loose reticulum. The protoplasm immediately round the nucleus has a granular appearance owing to the closeness of the reticulum. The connection between the ectoderm patch with the larger endoderm masses, as seen with a lower power, is shown in fig. 9, while fig. 6 represents two small endoderm masses connected together by, and giving off in all directions, fine strands as seen under a higher power.

The endoderm masses now begin to draw together (*vide* figs. 10—13, Pl. I), and form a ring-like mass applied all round the edge of the ectoderm patch. This ring-like mass is thicker at each end of the ectoderm disc than in the centre (Pl. I, fig. 12), where, indeed, it is sometimes interrupted (Pl. I, fig. 13). Pl. IV, fig. 16, represents a transverse section through the edge of an ovum at this stage.

The process of drawing together of the endoderm masses is still further continued and the ectoderm cap becomes bent round the concentrated solid mass so formed (Pl. I, fig. 15). Pl. IV, fig. 20, represents a transverse section through an ovum at a slightly later stage, in which a cavity, the future mesenteron, has begun to appear.

The ectoderm cap now gradually (Pl. I, fig. 18) grows round the endoderm mass, and almost completely encloses it. The one unenclosed point persists as the blastopore (Pl. I, fig. 20). While this process has been taking place the cavity in the endoderm mass has become larger, and on the completion of the process of epibole opens to the exterior through the blastopore. The ovum has now reached the gastrula stage (*vide* Pl. I, figs. 19 and 21).

Before passing on to consider the structure of the gastrula and the formation of the mesoderm, I desire to call attention to certain remarkable features in the preceding development.

1. The embryo at the gastrula stage, and in all the

earlier stages of development, is a syncytium. I have already pointed out that the segmentation is not a true segmentation. The segments do not separate from one another, but remain connected by a loose protoplasmic network. What happens is this: the nucleus of the fertilised ovum divides and gives rise to the nuclei of the two first segments. This causes a redistribution in the arrangement of the protoplasmic network, but no break in its continuity. In the unfertilised ovum there is only one centre—the nucleus—around which the protoplasmic reticulum is especially dense; while in an ovum with two segments there are two points—the two nuclei—around which we find an especial closeness of the reticulum. In an ovum with four segments there are four points around which the reticulum presents this especial density, and so on to the close of segmentation (Pl. I, figs. 1, 4, 5). In each case the centre is occupied by a nucleus derived by division from the nucleus of the fertilised ovum. But this is not all, and I come to the second remarkable feature I wish to mention.

2. No part of the nucleus or centre of force of the unsegmented ovum enters the clear endoderm masses. Its products remain confined to the ectoderm cells. The endoderm masses are, during the segmentation stages, without any structure resembling a nucleus as ordinarily described, and they do not acquire one till the disco-gastrula stage when the endoderm masses are beginning to aggregate (Pl. IV, fig. 16.) The endodermal nuclei, when they do appear, differ considerably in structure from the nuclei of the ectoderm. They are larger and have a very irregular shape; and further, they do not present the usual karyokinetic figures so characteristic of a dividing nucleus, but divide directly.

We may therefore look upon the ovum of the Cape Peripatus as presenting two different modes of segmentation, neither of which are instances of complete cleavage in the ordinary acceptation of the term.

First, there is the segmentation preceded and apparently determined by the division of the nucleus of the fertilised



ovum and its products. This process gives rise to the ectoderm cells.

Secondly, there is the division of the larger and clearer vegetative part of the ovum into the endoderm masses. This process takes place contemporaneously with the first, but apparently without being governed by the dividing nucleus of the animal or ectodermic part. At any rate no part of the latter enters the endoderm masses. It is true that the endoderm masses in the fresh state do present a central opaque portion (Pl. I, fig. 8), but I was unable by any of the staining methods I adopted (borax-carmin, hæmatoxylin) to find any trace of a structure like an ordinary nucleus in preserved specimens of the segmenting stages, though nuclei were easily visible in the endoderm of the gastrula and later stages. I did find, however, in my stained section of preserved segmenting ova, that the endoderm masses presented a central portion in which the spongework was much denser than in the peripheral parts (Pl. IV, figs. 16, 17). But this central denser portion was entirely without the especially deeply-staining chromatin so characteristic of the ordinary nucleus. This is especially shown by fig. 16. On the other hand, there are in the strands of the network of the endoderm masses small particles of a deeply-staining matter, which are neither visible in the unsegmented ovum nor in the gastrula stages, and which are not to be distinguished from nuclear chromatin. These deeply staining bodies are found in great numbers in the endoderm masses (fig. 16), and to a very small extent in the ectoderm cells. Have these central dense portions of the endoderm masses and the scattered deeply-staining bodies any hand in giving rise to the undoubted nuclei which subsequently appear? In other words, are these structures to be looked upon as nuclei in a condition of structure somewhat different from that usually presented by nuclei? or are the nuclei of the endoderm cells derived from the nuclei of the ectoderm by migration from the latter at the disco-gastrula stage? The continuity between the reticulum of the endoderm and ectoderm cells is retained as I have said through the disco-gastrula stage (fig.

16) to the gastrula stage (figs. 20, 24—26); indeed, in the gastrula stage it becomes, in consequence of the closer approximation of the endoderm masses to the whole inner surface of the ectoderm cap (fig. 20), still more marked. The strands of the reticulum of the ectoderm cells are continued into the strands of the ectoderm masses, and the whole ovum presents the appearance of a multi-nucleated vacuolated mass (fig. 20). It may be that some of the nuclei of the ectoderm cells pass along these continuous strands into the endoderm. But against this view are these two facts: (1) I have never seen any trace of such a migrating nucleus, and (2) the structure of the endoderm nuclei of the gastrula stage is so very unlike that of the ectoderm nuclei. Compare Pl. V, figs. 24—26.

Before leaving this subject, I may call attention to the small bodies present in the endoderm masses in the early gastrula stage (fig. 20). These bodies do not stain so deeply as the endodermal nuclei, which are now present in small numbers, or as the small, deeply-staining bodies seen in the sections of the disco-gastrula stage (Pl. IV, fig. 16); but they stain more deeply than the ordinary protoplasmic reticulum. Can these bodies have anything to do with the endodermal nuclei which are now appearing?

This subject is one of extreme interest, and I shall return to a consideration of it when I have described the structure of the nucleus of the unsegmented ovum and its immediate descendants.

3. The third point of interest in the development of the gastrula is the mode of origin of the cavity of the gastrula.

The solid gastrula consists of a multi-nucleated, much-vacuolated mass of protoplasm. The gut of the gastrula arises from an enlargement and confluence of the vacuoles in the centre of this mass. The gut of *Peripatus* is therefore to be looked upon as a vacuole, resembling in all essential respects the cavity in the body of a ciliated Infusorian. I refer to Pl. IV, fig. 20, which represents a section through a gastrula in which the gut is only just appearing, and to Pl. V, figs. 23, 24, which represent

sections through a rather later stage, in which the gastrula cavity is established. In fig. 23 especially, the gut is seen to be traversed by a protoplasmic reticulum containing a nucleus, and the blastopore itself to be partially choked up by a similar reticulum. The latter feature is also seen in fig. 24 *b*, a section of a slightly older embryo, and, indeed, is characteristic of all the later gastrula stages until the definite division of the blastopore into the primitive mouth and anus. The gut vacuole, soon after its appearance, acquires an opening to the exterior through a point on the surface where the ectodermal nuclei are and always have been absent.

#### THE VARIOUS FORMS OF NUCLEI IN THE EARLY STAGES OF DEVELOPMENT.

I have no observations on the nucleus of the ripe ovum. The facts which I have to record on the structure of the nucleus after the entrance of the spermatozoon may be described under the following heads:

1. The nucleus of the unsegmented ovum after the conjugation of the male and female pronuclei of the ectoderm cells in the early stages of segmentation.
2. The nucleus of the ovum before this event, but after the entrance of the spermatozoon.
3. The nucleus of the ectoderm during the segmentation and gastrula stages.
4. The endodermal nuclei.

1. The nucleus of the completely fertilized ovum and its immediate descendants is so large and favorable for study that I have decided to describe it first. It varies considerably in shape and structure in different ova. These variations no doubt represent different phases in the life-history of the nucleus. It has been impossible for me with the small number (ten) of unsegmented ova at my disposal to determine their sequence. I have, however, seen it in four conditions,



which differ from one another sufficiently to merit a special description; three of these were found before the beginning of segmentation, and one in an ovum of two segments.

*a.* A spherical structure (diameter, 0.04 mm.) bounded by a membrane, which is slightly indented at one point, where it sends in a prolongation of itself, which passes through the nucleus to become continuous with the membrane of the opposite side (Pl. III, fig. 8 *a*). The prolongation of the membrane across the nucleus is also connected with the membrane at another point (on the lower side of the figure), and, in addition, sends off processes which ramify in the substance of the nucleus. The nucleus is made up of a fine spongework of very pale fibrils, which are continuous with the nuclear membrane and with the septum and its processes just mentioned. In this spongework are a number of deeply-staining more or less spherical bodies.

The membrane, septum, and its processes stain about as deeply as the strands of the extra-nuclear reticulum, and they appear to be continuous with the fine, pale, little-staining strands, which constitute the main mass of the nuclear spongework. The pale spongework further possesses, as I have already said, a number of bodies—some elongated and branched, others globular—which are, I think, stained rather more deeply than the membrane and its offshoots, and which are likewise continued into the strands of the pale nuclear network. This latter fact is quite easy to see in the elongated branched staining fibrils, and the deeply-staining globular bodies, when carefully examined with a high power, present in many cases an angular appearance, the angles being continued into the pale reticulum.

As already stated, the nuclear membrane and septum appear precisely similar in structure to the strands of the external protoplasmic reticulum, and the latter are continued directly into the former. The pale nuclear reticulum is also similar to the extra-nuclear reticulum, differing only in intensity of staining.

It is also directly continued into the nuclear membrane and

septum. The apparently isolated, deeply-staining bodies, both globular and branched, are also, as I have said, continuous with the pale reticulum; so that this nucleus may be described as consisting of a portion of the spongework of which the ovum is composed, the nuclear protoplasm differing only from the external protoplasm in the fact that the staining matter is aggregated into special parts of the spongework instead of being uniformly diffused throughout the latter as in the extra-nuclear protoplasm. The apparent nuclear membrane is simply part of the protoplasm at the junction of the modified (nuclear) and unmodified (cell-substance) part of the protoplasmic network.

The question now presents itself; why do parts of the nuclear spongework appear more deeply stained than the rest? Either the parts thus staining are of greater mass than the rest, extending through the whole thickness of the section, while the pale strands are so fine that several of them, separated by the spaces of the meshwork, lie above one another in one transverse section; or there is a special chromatic substance, distributed at intervals in the intra-nuclear spongework. If the former is the correct answer the difference in colour between the pale and stained parts of the network is of the same nature as the difference in the colour of blood or any other coloured fluid when viewed in a thick or in a thin layer.

Though there may be something in this way of looking at the deeply staining parts of the nuclear spongework, I do not think that it entirely explains the matter.

It may here be mentioned that the meshes of the extra-nuclear reticulum immediately around the nucleus are much smaller than in parts remote from the nucleus, so that in a transverse section several strands will lie one above the other in even the thinnest section, while away from the nucleus, where the meshes are coarser, a smaller number of strands will coincide. Hence the protoplasm immediately around the nucleus appear more deeply stained than do the peripheral portions.

*b.* A form closely resembling the above, except in the fact that the nuclear spongework is stained slightly, though not quite so deeply as, some of the extra-nuclear protoplasm (Pl. III, fig. 2). There are only three (in the whole nucleus) small deeply-staining masses, which are not so conspicuous as in the first form, but are more deeply stained than the membrane and septa.

Using the second of the two above-mentioned alternatives, we may state the difference between these two nuclei thus: in the first form the chromatin of the nucleus is aggregated into a number of small masses, while in the second form the chromatin is, for the most part, diffused throughout the nuclear reticulum. The word chromatin being used to denote the property which enables the protoplasm to take up and retain the staining matter. The extra-nuclear protoplasmic threads possess this property, and may be said to possess chromatin, but it is in a diffused form, as in the second form of nucleus.

*c.* In the third form (Pl. III, fig. 3) the nucleus is divided by a number of septa, radiating from its centre, into chambers. The chambers are partially divided up into secondary chambers by prolongations of the septa. The septa are continuous externally with the extra-nuclear protoplasmic reticulum. It is impossible to speak of a distinct boundary of the nucleus in this form, and the substance of the nuclear septa and of their prolongations is exactly similar in appearance and staining properties to the strands of the surrounding protoplasmic network or spongework.

A number of chromatin masses occur in each chamber of this radiate nucleus—they appear to lie in the offshoots of the septa into the chambers and in delicate expansions of these. But it is impossible to determine exactly the relation of these chromatin globules to the protoplasmic network in the nucleus.

This form of nucleus is most interesting, because were it not for the chromatin masses the nucleus would be quite undistinguishable from the surrounding protoplasm, except, perhaps, by the fact that the meshes of the network (i. e. network as



seen in section) are rather larger than in the protoplasm immediately around the nucleus.

The most important, and at the same time most certain, of these observations on the nucleus of the fertilised ovum of *Peripatus*, is that the intra-nuclear and extra-nuclear reticulum are both continuous with the so-called nuclear membrane. This continuity between the extra-nuclear and nuclear spongework is rendered still more obvious by a consideration of the next form.

*d.* The last form I have to describe under this head is the spindle form (Pl. III, fig. 11). It was met with in an ovum of two segments.

The spindle is of enormous size (distance between the poles 0.06 mm.). The protoplasmic fibres composing it are absolutely the same in appearance as the rest of the cell protoplasm, from which they must have been largely derived. The chromatin is present in a very condensed form (i. e. deeply staining) as a number of bent rods at the equator of the spindle. Around the poles of the spindle the protoplasmic reticulum is arranged in a radiate fashion. The spindle appears not to be composed of simple fibres running from pole to pole, but of the ordinary reticulum, the meshes of which are very much elongated in a direction parallel to the long axis of the spindle. The same may be said of the fibres radiating from the poles of the spindle.

The facts which are most clearly brought out by the above observations, and about which I have no doubt, are—

1. The continuity of the nuclear reticulum with the extra-nuclear reticulum.

2. The similarity in structure between, and, the continuity of the so-called fibres of the spindle in form *d* with the surrounding reticulum; and the conclusion I have drawn from my observations is, that the nucleus of the fertilised ovum of *Peripatus* differs from the cell protoplasm only in the manner in which the so-called chromatin contained in the protoplasmic meshwork (both of nucleus and rest of ovum) behaves. In the nucleus it varies from a state of diffusion through the

reticulum to a state in which it is condensed into the chromatin masses of forms *a*, *c*, and *d*.

In the subsequent stages of segmentation the nucleus gradually becomes smaller until at the close of segmentation it has an oval form with a long diameter of 0.016 mm. It now presents the features described by Flemming and other observers in the nuclei of the salamander and other animals.

During segmentation the nucleus generally has the third form above described: I have never seen it in a spherical, and only once in a spindle form. I conclude that these forms, if they occur, are very rapidly passed through.

2. The Female and Male Pronuclei.—I include under this head the nucleus of the ovum after the formation of the first polar body. I have no observation on the nucleus of the uterine ovum before this event.

*a.* Two Ova of *Peripatus Balfouri* with one polar body completely formed and no trace of the second.—In one the nucleus of the ovum had the spindle form and the two equatorial rows of chromatin bodies had already slightly separated from one another. It was placed near and with its long axis parallel to the surface of the ovum. The area of dense protoplasm in which it was placed was considerably smaller than in later ova which possessed the first segmentation nucleus. The spindle had a length from pole to pole of .017 mm. It presented precisely the same features of structure as the larger spindle described above.

In the other ovum the nucleus had the form of a number of closely aggregated masses of chromatin occupying an area of .0084 mm. The protoplasm in which these masses were contained did not appear to differ in any way from the rest of the denser protoplasm of the animal pole.

Male Pronucleus.—On the side of the ovum opposite to the nucleus, and nearly in the same transverse plane, was a small lobed mass of chromatin having a diameter of .0042 mm. It was contained in a very small area of protoplasm in which the network was dense as at the opposite pole. This I take to be the male pronucleus.

Finally, this ovum possessed the peculiarity of presenting in surface views (Pl. I, fig. 3) a number of opaque patches. These in section are seen to be due to a number of peripherally placed areas in which the protoplasmic reticulum was dense as it is around the female nucleus. The protoplasmic reticulum of these denser areas was arranged in a radiating manner around a central point; it presented no deeply-staining masses of chromatin.

*b. Two Ova in which the second polar body was being formed.*—In both of these the nucleus of the ovum had already divided into the definite female pronucleus and the nucleus of the second polar body, which in each case was attached by a wide base to the ovum. In one, however, this division has only just occurred, and the female pronucleus was in the form of some small deeply-staining masses placed close to the surface of the egg; the denser protoplasmic reticulum of the animal pole around them not being apparently modified. The male pronucleus presented the same features as in the last described ovum.

In the other ovum the female pronucleus (Pl. III, fig. 1) was in a very different condition to the above. The chromatin masses had acquired a definite relation to the protoplasmic reticulum, and the whole structure resembled in all its essential features the chambered nucleus of the fertilised ovum (see above, p. 31). Its greatest diameter was  $\cdot 029$  mm. At the opposite side of the ovum and not quite in the same plane (though for the sake of convenience the two structures are combined in one figure), there was a large ( $\cdot 025 \times \cdot 016$  mm.) reticulated structure, which I take to be the male pronucleus (Pl. III, fig. 1). This male pronucleus was much nearer the centre of the egg than those previously described, as though it were in the act of moving to the female nucleus. The network in this nucleus was of varying degrees of fineness, and was more deeply stained in some parts than in others; the main strands were obviously continuous with the surrounding membrane, which in its turn was obviously continuous with the very loose reticulum outside.



I have no observations on the transformation of the simple male pronucleus of the early stages into this complicated structure, nor have I any on the transformation, quite as remarkable, of the few chromatin masses, which represented the female pronucleus in the last described ovum, into the complicated structure present in this case.

3. The Nucleus of the Ectoderm in the gastrula and later stages.—I have already (p. 33) said all that I at present have to say about this nucleus. It is much smaller than the earlier nuclei, and not specially favorable for study. I have little doubt, however, that the network of which it is composed is continuous with the external spongework.

4. The Endodermal Nuclei.—As I have already said there are apparently no nuclei in the endoderm masses of the segmenting ovum, or, in other words, no part of the first segmentation nucleus enters, so far as I could see, these masses during the segmentation. At any rate there can be, I think, but little doubt on one point, viz. that the endoderm masses do not during the segmentation contain any structure like a nucleus as ordinarily described. They do contain, as I have already said, a densely reticulated central area, but this is without any deeply-staining chromatin so characteristic of a nucleus. Can this area represent a nucleus, perform the functions of a nucleus for these endodermal masses?

Without venturing to decide the question I may draw attention to two facts brought out by the study of the large nuclei described under heading 1 (p. 28). These are: (1) The nuclear spongework is perfectly continuous with the extra-nuclear spongework, and (2) the amount of concentrated deeply-staining matter may be very small, as in the undoubted nucleus of fig. 2 in which the three masses in the figure represented the whole of the especially deeply-staining matter present.

The question, therefore, presents itself; what is the essential part of the nucleus? Is it the spongework or is it the deeply-staining parts of the spongework? A comparison of figs. 2 and 3, Pl. III, in which the amount of deeply-staining matter is so different, favours the first view, viz. that the essential part of

the nucleus is the spongework ; while on the other hand the facts about the male and female pronuclei described on p. 33 are in favour of the second view, viz. that the deeply-staining matter is the all important part of the nucleus. For in the latter cases we have a stage in which the nucleus is represented only by a mass of deeply-staining matter, which subsequently enters into a more complicated relation with the surrounding reticulum in order to give rise to the vesicular form of nucleus ordinarily found.

It is, therefore, impossible to decide which, if either, of these two views is correct. Indeed, it seems useless to discuss the matter except in connection with the functions of the nucleus. The nucleus appears to be a kind of co-ordinating centre for a given mass of protoplasm, and as such it may be looked upon as a centre from which force emanates. If this is so, need it have any essential structure beyond being the point to which all the strings of the protoplasmic spongework converge—in other words, such a structure as that possessed by the two poles of the spindle in Pl. III, fig. 11? Is it not conceivable that a centre of this kind is necessary to the well-being of all masses of protoplasm beyond a certain size ; and that if they do not derive such a centre from a pre-existing centre they acquire one *de novo*? May not the complexity of structure which the nucleus ordinarily presents be a secondary feature, and indicative of a higher organization of the protoplasmic mass containing it? Or, to put the matter in another way, is the complicated structure of the nucleus as ordinarily seen the cause or the result of the peculiar properties of the nucleus?

Without venturing to put forward any hypothesis on this difficult and obscure matter, I may draw attention to a fact which favours the view that the nucleus of any protoplasmic mass is primarily a central and complicated nodal point to which the strands of the spongework mainly converge, and that the more complicated and apparently vesicular structure which it generally presents is a secondary feature. The fact I refer to is this: the first products of the division of the nucleus, i.e. the earliest stage of the two new nuclei—I mean the poles

of the spindle—are simply nodal points around which the spongework is radiately arranged, and are without any of the complexity of structure which they subsequently acquire.<sup>1</sup>

I now pass to the structure of the undoubted endodermal nuclei which appear at the disco-gastrula stage. They are usually larger than the ectodermal nuclei (see figs. on Pl. V), and are sometimes very large. They are nearly always of an angular shape, and sometimes they are branched. They consist of a fine network, which stains, and the strands of which at certain points are thickened and give rise to nucleolar-like bodies. The strands of the network are continuous with the membrane, which is itself continuous with the strands of the extra-nuclear reticulum. There is no increase in the density of the extra-nuclear reticulum round the nucleus, in fact, rather the opposite. These endodermal nuclei appear to divide directly, and they never present the figures so characteristic of the indirect division. I have figured on Pl. III, figs. 4 and 5, some peculiar endodermal nuclei found in a young hollow gastrula. Fig. 4 differs from the ordinary endodermal nuclei in the great development of its branching processes, which appear to be continued into the strands of the extra-nuclear reticulum, and in the fact that two of them are connected by processes. Fig. 5 is peculiar for the large size, number, and peripheral arrangement of the larger staining-bodies.

#### THE STRUCTURE OF THE GASTRULA.

The fully developed gastrula is, as I have already mentioned, a syncytium. Its cavity is a vacuole derived by the enlargement of one or the fusion of several of the vacuoles of the mass of endoderm. The whole embryo at this stage (Pl. V, figs. 24 *a—d*) is vacuolated, the ectoderm as well as the

<sup>1</sup> For an account of observations on the supposed spontaneous origin of nuclei during development, I may refer to Balfour, 'Comp. Embryology,' vol. i (2nd ed., p. 108). The ova in all the cases there cited are large-yolked and meroblastic.



endoderm, but the vacuoles of the endoderm are the largest. There is generally a special layer of vacuoles beneath the ectodermal nuclei, between which strands of protoplasm pass from the ectodermal to the endodermal reticulum.

The blastopore is a slightly elongated structure (Pl. I, figs. 19, 21), and is itself traversed by a loose protoplasmic reticulum (Pl. V, fig. 24 *b*). The endodermal layer lining the gut sends out a few processes into the gut which anastomose with the blastopore reticulum. The gut of young gastrulæ contains a largely developed reticulum (Pl. V, fig. 23), the remains of the previous stage. In older gastrulæ there may sometimes be seen apparently isolated masses of protoplasm (Pl. V, fig. 24 *a*), which, however, are probably connected with the endodermal lining and eventually drawn into the latter.

Just in front of the blastopore there is a large number of nuclei in the middle ventral line (Pl. V, fig. 24 *a*).

Behind the blastopore there is a special area of ectoderm in the middle line which I have called the polar area, and which possesses the following characteristics: close behind (Pl. V, fig. 24 *c*) the surface is flat and, if anything, marked by a slight groove, the nuclei are more columnar than elsewhere, and there is a larger quantity of protoplasm outside the nuclei than in most other parts of the ectoderm. Further back (Pl. V, fig. 24 *d*) there is in the middle line a fairly large area of protoplasm containing one or more large round nuclei.

The polar area extends from the blastopore backwards for a distance in this embryo (figured on Pl. I, fig. 21) of about .07 mm. The nuclei in this area will give rise to the nuclei of the primitive streak.

The protoplasm of the polar area is vacuolated in the ordinary way. Fig. 21, Pl. IV, represents a drawing under a higher magnifying power of the hinder part of the polar area of this stage.

Figs. 22 *a—c*, represent a series similar to the above through the polar area of a rather older embryo. The front part of

the polar area has a well-marked groove (Pl. IV, fig. 22 *a*) which is the primitive groove.

#### FORMATION OF THE MESODERM.

The nuclei of the mesoderm are derived from the nuclei of the polar area. The latter increase largely in number (Pl. V, fig. 25 *b*) and form a primitive streak. An early stage of this process is shown in figs. 22 *a*, *b*. It begins at the front end of the area, but soon the nuclei of the whole area are implicated. They are constantly met with in a state of division.

In the next stage, stage A, figured on Pl. I, fig. 22, a well-marked primitive streak is visible when the embryo is examined from the surface.

A series of sections through such an embryo (Pl. V, figs. 26 *a—d*) show that the blastopore is still traversed by a reticulum (figs. 26 *a*, *b*), and that the primitive streak is largely developed (figs. 26 *c*, *d*), and its front part traversed by a well-marked groove. In the deeper parts of the primitive streak, at about the middle of its length, there is an area of protoplasm containing two (perhaps more) nuclei, and characterised by the relative predominance of the extra-nuclear protoplasm. This area is shown in section in fig. 26 *d*. I cannot help thinking that it is derived directly from the hinder part of the polar area of the previous stage figured in Pl. IV, fig. 21, and Pl. V, fig. 24 *d*. It seems to me that while the nuclei of the polar area on each side of this structure constantly undergo division (fig. 22 *c*, 24 *d*) the nuclei in this structure do not divide, but that it becomes overgrown ventrally by the proliferating lateral nuclei of the polar area (Pl. IV, fig. 21), and thus comes to acquire a deeper position. This would seem to imply that the growth of the mesodermal nuclei in the hinder part of the polar area is a bilateral process, that the cells on each side of the middle line only proliferate; and I think that a careful examination of the anterior part of the polar area

shows that the growth of nuclei there also is a bilateral one, though the bilateral nature of the growth is not so obvious as it is behind. The reason of this is that behind there is a median structure—the hinder part of the polar area with its round nuclei—on each side of which the growth appears to take place, while in front there is no such well-marked median structure, but there is the groove; and I think that a careful examination of the relation of the growing nuclei to this groove shows the bilateral nature of the growth. I refer in support of this to figs. 22 *a*, 25 *b*, 26 *c*, which are all sections through the front part of the primitive streak, fig. 22 *a*, being of course from the youngest of the embryos; and to figs. 25 *a*, 26 *b*, which are in each case the last section through the blastopore. It is difficult to say whether 25 *a* is to be regarded as passing through the hind end of the blastopore or through the front end of the streak, but it presents nuclei, which must be regarded as mesodermal, in a position which is consistent with the view that they have been derived from the row of nuclei which extend between the ectodermal and endodermal nuclei.

Again, in fig. 26 *b*, we see similarly placed nuclei in the act of division, with what must be regarded as mesodermal nuclei on their inner borders.

Further back (figs. 22 *a*, 25 *b*, 26 *b*) the blastopore is represented only by the groove, and it is more difficult to satisfy oneself on the point.

However, I am inclined to think that the growth of primitive streak nuclei is a bilateral one, in the anterior as well as in the posterior part of the primitive streak, though I admit that the evidence in favour of this view is not entirely satisfactory.

If I am correct in this supposition, and in my conjecture that the primitive groove is a rudimentary posterior part of the blastopore (it is so considered in other tracheate embryos), then the development of the mesoderm in *Peripatus* consists in an ingrowth of nuclei from the lips of the blastopore and resembles that described in so many other forms.

The mesodermal nuclei of the primitive streak now grow



forward in two bands—one on each side—between the ectoderm and endoderm (Pl. V, figs. 26 *a* and *b, mb.*). They seem to arrange themselves on the strands, connecting the ectodermal and endodermal reticulum, and they constitute the mesoblastic bands. A series of vacuoles are formed in these bands, around which the nuclei arrange themselves in rows, thus giving rise to the mesoblastic somites.

The further development I shall describe in the next chapter.

#### SUMMARY AND GENERAL CONCLUSIONS.

The Segmentation is apparently complete, the ovum appearing to divide into ectoderm and endoderm cells.

The so-called endoderm cells are at first without a distinct nucleus, they do not get a nucleus until just before the gastrula stage.

All the cells of the ovum, ectodermal as well as endodermal, are connected together by a fine protoplasmic reticulum, which is placed, as are also the cells, immediately beneath the egg membrane, and therefore around a central space.

Each ectoderm cell consists of a central nucleus around which is a close protoplasmic spongework, which, at the outer parts of the so-called cell, becomes of a gradually looser nature until it runs into the spongework of the surrounding cells.

Each endoderm mass consists of a central denser spongework which gradually becomes looser towards the periphery of the mass until it is continued into a fine reticulum. The endoderm masses are far apart from each other and are connected by this reticulum.

The continuity of the various cells of the segmenting ovum is primary and not secondary, i. e. in the cleavage the segments do not completely separate from one another. But are we justified in speaking of cells at all in this case? The fully segmented ovum is a syncytium, and there are not and have not been at any stage cell limits. I think the cleavage should be rather described not as segmentation,

but a multiplication of the nucleus or centre of force which causes a corresponding readjustment in the density of the network at different parts of the ovum, but no break in continuity.

The Gastrula arises by a process of epibole and is at first solid.

The endoderm masses at first have no nuclei. Nuclei first appear in them during the progress of the epibole by which the gastrula is formed. I have not been able to determine the origin of these nuclei. They either arise *de novo* in the endoderm masses or migrate into the latter from the ectoderm. The protoplasmic network at the centre of each endoderm mass is denser than at the periphery, but is without the chromatin granules, so characteristic of a nucleus. But I have described a stage of the nucleus in the fertilised unsegmented ovum in which the chromatin granules are almost entirely absent, and in which the network presents no essential difference from the surrounding network. Again, another in which the nuclear network merges so gradually into the surrounding network, that it is impossible to point to any limit between them. I therefore think it quite possible that this central denser protoplasm in the endoderm masses may give rise to the nucleus which subsequently appears.

The gastrula is a syncytium; the ectodermal nuclei are arranged around the periphery of the ovum, while the endodermal nuclei are within. The latter are characterised by their angular shape, and by never presenting the karyokinetic figures characteristic of the ectodermal nuclei. The protoplasm of this syncytium is much vacuolated throughout, but the vacuoles are largest in the centre. These central vacuoles unite and give rise to the gut cavity, which opens to the exterior through a point on the surface where the ectodermal nuclei have always been absent. This opening is the blastopore. The blastopore, until quite late in development, is traversed by protoplasmic strands, which anastomose with similar strands projecting from the protoplasm lining the large central vacuole or gut.

The gut of *Peripatus* arises, therefore, as a vacuole in a multinucleated mass of protoplasm, and the gastrula of *Peripatus* is a multinucleated mass or syncytium, with absolute continuity of the protoplasm of all parts of the ovum.

**The Mesoderm.**—After the definite formation of the blastopore, an area of protoplasm, placed in the ectodermal layer of the syncytium, and characterised by possessing several nuclei less densely packed together than elsewhere, is distinctly visible in the middle line of the ventral surface just behind the blastopore. This area I have called the polar area. Its nuclei undergo division and give rise to the densely packed mass of nuclei of the primitive streak. A part of it seems to persist for some time in the deeper parts of the primitive streak close to the endoderm.

The nuclei of the primitive streak migrate forwards between the ectodermal and endodermal nuclei, and take up their position in the protoplasm intervening between the latter.

These rows of nuclei are the mesodermal bands. They soon arrange themselves into groups around a central vacuole, and so give rise to the most conspicuous parts of the mesoblastic somites. I leave the ovum for the present at the commencement of the formation of the somites, merely stating that it is still a syncytium.

There are a certain number of facts in the above account which are of general interest and seem to deserve more discussion so far as their relation to processes in other forms are concerned. These are :

1. The connection between the intra- and extra-nuclear reticulum.
2. The segmentation.
3. The origin of the gut as a vacuole.
4. The syncytial nature of the embryo.
5. The origin of the mesoderm.

I propose to consider the first four of these points at once, and to defer the discussion of the 5th to the next chapter.

A. The nucleus of the unsegmented ovum and of the early stages of segmentation of the Cape *Peripatus* are particularly



favorable for study, because of their large size and the rapid changes which they undergo. Unfortunately I have not, so far, been able to make out the sequence of these changes.

It is a disputed point as to whether or no the nuclear and extra-nuclear reticula are continuous. Leydig (12), Stricker (16), Klein (9, 10, 11), and Heitzmann (5), hold that they are. So far as the nucleus of the early segmentation stage, and of the endoderm of *Peripatus* is concerned, I am able fully to confirm the views of these observers.

The general views I hold with regard to the nucleus are stated on p. 32 and I need not repeat them here. I only desire to point out that the opposite view, viz. that the nucleus is isolated so far as continuity of protoplasm is concerned, is, from a physiological point of view, very difficult to accept; and I think that the burden of proof rests with him who maintains it.

The peculiar lobed structure (Pl. III, fig. 3) of certain stages of the nucleus has been described before by other observers, notably by Balfour in his "Monograph on the Development of Elasmobranch Fishes," in the early stages of development.

Klein in his communication on this subject, refers (10, p. 175) to and confirms Stricker's (16) observations on the contractility of the nuclear spongework and its continuity with the extra-nuclear spongework in the colourless blood-corpuscles of the newt and frog. He further confirms Stricker's statement as to the disappearance of the nuclear membrane, and himself adds: "The nucleus is therefore a part of the cell substance specially differentiated by the presence of a membrane." Presumably Dr. Klein would still speak of a nucleus when the membrane is absent. I am not able to make out Klein's views with regard to this membrane. He says (11, p. 415): "In the convolution and basket of daughter nuclei the membrane is very indistinct and is also here due to the close position of the fibrils." I infer from this that he regards the nuclear membrane as a part of the general reticulum at the junction of the nuclear and extra-nuclear parts of the reticulum, which gets in certain stages of the nucleus a regular ar-

rangement. This at any rate is my view for the *Peripatus* nucleus.

Klein figures (10, Pl. 18) nuclei from the epidermis of the newt in a state of direct division. These figures resemble very closely some of the endodermal nuclei in the gastrula of *Peripatus*.

Klein is still more explicit as to the continuity of the nuclear and extra-nuclear reticulum in his second communication on this subject (11, p. 416).

Unfortunately I have not been able to see the papers of Stricker and Heitzmann.

Leydig in his latest communication (12) regards the spindle-fibres as parts of the ordinary reticulum (spongioplasma he calls it) with much elongated meshes (p. 9). He further looks upon the nuclear membrane as merely the outer portions of the nuclear network, and describes it as being porous, and takes the same view as Klein with regard to the continuity of the nuclear and intra-nuclear network.

Leydig also describes some accessory nuclei as occurring in certain cells. These are smaller than the main nucleus and stain less deeply. It is possible that they are structures of the same nature as those described above in the endoderm of *Peripatus* (*vide* pp. 26, 27).

He refers, in this connection, especially to the small accessory nuclei which are found in many Protozoa, and which, according to Gruber (3) and Jickeli (7), are for the most part derived from the breaking up of the main nucleus. The particles resulting from this fragmentation of the nucleus seem eventually to come together again to form a new main nucleus. One would like to have some more details about this peculiar process in Infusoria, derived if possible from the study of sections. The term "fragmentation," which is applied to it apparently because the chromatic parts of the nucleus become separated from one another and scattered throughout the animal, seems to imply a distinct breaking up into small isolated portions. If this really happens the nucleus of Infusoria must differ from most other nuclei in which the chromatic

matter is a part of the nuclear network, which is itself continuous with the extra-nuclear network. I should be inclined to look upon the process as an increase in size or extension of the nucleus, such as seems to have been described by Stricker in certain leucocytes.

Pfitzner (14), on the other hand, strongly maintains the isolation of the nucleus during the whole of its life-history, and he recommends certain reagents to demonstrate this fact. But inasmuch as he himself admits (p. 72) that these reagents produce great changes in the nucleus, his negative conclusions cannot be regarded as having so good a basis as the positive results of Klein and Leydig, whom I can thoroughly confirm in the matter.

I may draw attention in passing to the similarity of the branched endodermal nuclei of *Peripatus* to the nuclei of leucocytes figured by Pfitzner (14, Pl. V, fig. 21).

I have not been able to distinguish nucleoli in the nuclei of *Peripatus* as distinct from the chromatic thickenings of the spongework. Flemming (1) says that nucleoli proper participate in forming the chromatic figures in cell division. Flemming in his work on the cell and cell nucleus (1) has not seen the continuity between the strings of the nuclear and intra-nuclear spongework. He does not deny its existence but holds that it is not proved.

Flemming makes the important statement that the first change observable in a cell whose nucleus is about to divide is in the extra-nuclear protoplasm, the fibres of which arrange themselves radially around two points on opposite sides and at the circumference of the nucleus. Contemporaneously with this the nuclear network begins to change, and almost immediately afterwards the achromatic spindle-fibres appear in the nucleus.

These facts seem to point to the conclusion that the actual centre of force, of which the nucleus is the seat, divides first and is followed by the re-arrangement of the cell and nuclear protoplasm. Flemming considers that the nuclear network consists of an achromatic substance containing granules of



chromatin which have the power of moving about in the network. These chromatic granules are fairly uniformly diffused in the resting nucleus, but in a nucleus preparing to divide they aggregate together in certain parts of the network. The parts of the network from which the chromatin has gone become inconspicuous and form the achromatic spindle-fibres, while the parts into which it has gone form the conspicuous deeply-staining rod-like fibres, so characteristic of a dividing nucleus. The achromatic fibres of the spindle which begin to appear at the first sign of the division of the nucleus are, on this view, parts of the nuclear network. With this view I entirely agree. The structure of the various phases of the nucleus of the ovum of *Peripatus* will bear the same explanation, allowing for this difference, viz. the amount of chromatic substance in the ovum of *Peripatus* is much smaller—so small, indeed, that even in the resting stage (Pl. III, fig. 8) the chromatin is absent from the greater part of the network, which thus has the pale appearance of the achromatic fibres of Fleming, an appearance which is only found in the dividing nuclei of the salamander. The reason why achromatic fibres are so little marked in the resting nuclei of most animal cells is that they are masked by the large amount of chromatic substance they contain.

This view of the spindle-fibres is not at all opposed to Strasburger's contention (15, fig. 44) that part of them are derived from the extra-nuclear spongework; for the nuclear and extra-nuclear spongework are, as I have already maintained, continuous with each other; in other words, part of the same system.

I have seen nothing of any process corresponding to the splitting of the fibres; but this is not to be wondered at considering that I have only twice found the spindle stage of the nucleus.

B. It is becoming more and more clear every day that the cells composing the tissues of animals are not isolated units, but that they are connected with one another. I need only refer to the connection known to exist between connective

tissue cells, cartilage cells, epithelial cells, &c. And not only may the cells of one tissue be continuous with each other, but they may also be continuous with the cells of other tissues. For instance, I may refer to Fraipont's (2) work on the nervous system of the Archiannelida. He describes an intermuscular nervous plexus which is continuous with the muscle-cells and with the surface epithelial cells (2, Pl. 13, figs. 11, 16).

Instances of this kind might be multiplied from recorded observations, and are being multiplied day by day by histological observers to such an extent, that we are almost, if not quite, justified in regarding the body of an adult animal as a syncytium. It is true that the cells of the blood and lymph, and the ripe generative cells, are completely isolated. But the former, in their first stages of growth, form part of the syncytium; as in all probability do the latter also.<sup>1</sup>

This continuity, which for a priori reasons we should expect, has hitherto been regarded as a fact of little morphological importance and relegated to the category of secondary features. The ovum, it is said, segments into completely isolated cells; and the connection between these is a secondary feature acquired late in development. It has always been considered that the first stage in the evolution of the Metazoa was a colonial Protozoon, i. e. a mass of perfectly isolated unicellular organisms derived by complete division from a single cell.

Now, while I do not wish to exalt the facts of the cleavage and early development of *Peripatus* above recorded to a position of undue importance, or to maintain that of themselves they are sufficient to destroy this conception of the origin and structure of a Metazoon, I think I am justified in pointing out that if they are found to have a general application, our ideas on these subjects and others connected with them will have to undergo a considerable modification.

The ancestral Metazoon will no longer be looked upon as a colonial Protozoon, but rather as having the nature of a multi-

<sup>1</sup> I may refer in this connection to the processes of the follicular cells which perforate the zona of a mammalian ovum,

nucleated Infusorian with a mouth leading into a central vacuolated mass of protoplasm.

The continuity between the various cells of the adult—the connections between the nerves and muscles and sensory epithelial cells, receive an adequate morphological explanation; being due to a primitive continuity which has never been broken.

Herbert Spencer's view of the origin of the nervous system may perhaps not be so far from the mark as at first sight appeared. In any case the efforts to find out how the connection is established between the nervous and muscular tails of the ectoderm and endoderm of the lower animals should be transferred to the earliest phase of the embryo, i. e. to the segmentation stages.

Finally, if the protoplasm of the body is primitively a syncytium and the ovum until maturity a part of that syncytium, the separation of the generative products does not differ essentially from the internal gemmation of a Protozoon, and the inheritance by the offspring of peculiarities first appearing in the parent, though not explained, is rendered less mysterious; for the protoplasm of the whole body being continuous, change in the molecular constitution of any part of it would naturally be expected to spread, in time, through the whole mass.

In short, if these facts are generally applicable, embryonic development can no longer be looked upon as being essentially the formation by fission of a number of units from a single primitive unit, and the co-ordination and modification of these units into an harmonious whole. But it must rather be regarded as a multiplication of nuclei and specialisation of tracts and vacuoles in a continuous mass of vacuolated protoplasm.

At any rate I may safely say that, so far as the individual embryonic development of *Peripatus* is concerned, the connection of cell with cell is not a secondary feature acquired late in development, but is primary, dating from the very beginning of development.

Since making these observations on the syncytial nature of the cleavage and gastrula stages of *Peripatus capensis*, I



have examined other segmenting ova to see if the fact was one of general application, with negative results.

The cells of segmenting ova are generally so closely applied together and the protoplasmic strands so hidden by food-yolk, that it is difficult to be certain of the point either way. But with ova in which the segments are slightly separated from one another—and I believe there are such though I have never seen them—the observation ought to present no special difficulty.

Indeed it is a well-known fact that an incomplete separation of the cells is found in the early stages of the segmentation of centrolecithal eggs; but it has always been assumed that this was a temporary phase, and that the segments eventually separated. We now know, thanks to the researches of Heathcote (4), that this separation does not occur in the centrolecithal egg of the Myriapod, *Julus*; and it seems to me extremely probable that his results for this form will be found on careful examination applicable to other similar ova.

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## CHAPTER III.

### ON THE CHANGES FROM STAGE A TO STAGE F.

#### THE ECTODERM, ENDODERM, AND EARLY HISTORY OF THE SOMITES.

##### THE ECTODERM.

During Stage A, the ectodermal or outer part of the embryo consists of a closely reticulated protoplasm, which contains a single layer of oval nuclei of fairly uniform size. At the lips of the blastopore this layer, with its contained nuclei, is prolonged inwards for a short distance to the more vacuolated endodermal part of the embryo. These nuclei, which are arranged in a layer immediately within the lips of the blastopore, resemble in their shape the ectodermal nuclei (Plate VI, figs. 2, 3), and they may be regarded as ectodermal or endodermal according to the inclination of the observer. I am inclined to call them intermediate or undifferentiated nuclei, that is to say, nuclei which cannot be definitely assigned to the endoderm or ectoderm, and in this capacity I shall have occasion to return to them when I come to speak of the later history of the mesoderm.

The protoplasm surrounding these nuclei projects into the cavity of the blastopore and into the archenteron, in the form of delicate processes, which anastomose with other similar processes (Plate VI, fig. 3; Plate V, fig. 26 *b*).

When the mesodermal bands are formed, the nuclei of the ectoderm overlying them become slightly longer than elsewhere, and the ectoderm has the appearance of being composed of columnar cells. The nuclei are, however, still in a single layer.



At the beginning of Stage c, a number of smaller, more rounded nuclei appear in the ectoderm within the outer layer of oval nuclei (Plate VI, fig. 6 c). These nuclei are, in the next stage (Plate VI, fig. 9, *v.n.*), found along the inner i. e. ventral portion of the ectodermic thickening just mentioned as overlying the somites. They constitute the rudiments of the central nervous system.

The nuclei of the outer, i. e. latero-dorsal portions of the original ectodermal thickening (Plate VI, fig. 9), remain in a single layer, and the ectoderm containing them becomes pushed out by processes of the mesoblastic somites. These processes constitute the rudiments of the appendages. The latter are, as I have already mentioned in Ch. I, formed from before backwards, the first to appear being the appendages of the pre-oral somites—the later antennæ—which exactly resemble in their development the other paired appendages of the body.

After this general account I will now describe, in greater detail, the development of the ectoderm up to Stage e, under the following heads:

1. The dorsal and ventral ectoderm which intervenes between the lateral thickenings.
2. The lateral thickenings.
3. The ectoderm of the proctodæum and stomodæum.

It will be convenient to defer a description of the ectoderm of the primitive streak to the section of this paper on the history of the mesoderm.

4. The slime-glands.

1. **Dorsal and Ventral Ectoderm.**—During Stages a and b the ectoderm on the dorsal and ventral surfaces is composed of what may be called cubical cells with oval nuclei, but it must be remembered that these cells are not isolated from one another or from the endoderm. During Stage c, the nuclei of the dorsal ectoderm become spherical (Plate VI, fig. 6 c), as do also the nuclei of the ventral ectoderm on each side of the mouth (fig. 6 b). But the greater part of the ventral ectoderm, namely, that which intervenes between the mouth and anus

(Plate VI, fig. 6 *c*), and that which is placed on each side of the anus, becomes reduced to an extremely thin layer (Plate VI, fig. 6 *c, d*), the character of which will be obvious from an inspection of the figures. In Stages *d* and *e*, the ventral ectoderm retains the characters already described, but its width becomes less, the lateral thickenings having somewhat approached one another on the ventral surface (figs. 9, 25). The dorsal ectoderm, on the other hand, becomes in Stage *d* somewhat reduced in thickness (Plate VI, figs. 9—13), though it never becomes as thin as the ventral portion. Subsequently, in Stage *e*, it undergoes a striking change. It becomes much thickened. The thickening first appears in Stage *d* in the region of somites 7—10 (Pl. VII, fig. 25), where indeed it lasts longer and is more marked than elsewhere, and gives rise to the prominence marked *d* in the figures of Plate II. The change begins at the sides and gradually extends dorsalwards. The ectodermal hump (*d.*) seems to retain until its disappearance indications of this bilateral origin. The thickness of the dorsal ectoderm varies in different specimens, and no doubt depends to a certain extent on the amount of contraction which the protoplasm has undergone at death.

This increase in thickness is mainly due to the appearance, outside the nuclei, of a layer of vacuolated protoplasm. The vacuolation is not shown in my figures, but it is a very striking feature. The surface of the dorsal ectoderm, particularly of the hump, is very rough in these stages, and in the best-preserved embryos without a definite external boundary. It presents very much the appearance which a bath sponge would present in section, fraying out, as it were, into the surrounding fluid; and one may fairly conclude that during life it possesses the power of sending out processes into the fluid surrounding the embryo, and that the superficial vacuoles open to the exterior. In short, I am inclined to think that this surface ectoderm during Stages *e* to *f* has a nutritive function, absorbing the fluid in which the embryo lies, and it seems to me conceivable that the placenta described by Kennel in the Trinidad species may be a more specialised organ of the same nature. During the pro-

gress of Stage F the nuclei which have hitherto been placed in the deep parts of the layer (Plate VII, figs. 23 *a—e*, 25) acquire a superficial position, excepting in the hump, where they retain their deep position until after Stage G. Contemporaneously with this change the deeper parts of the ectoderm become filled with very large vacuoles, so that the protoplasm is reduced to fine cords, passing inwards from the superficial nucleated layer. This vacuolated deeper part of the dorsal ectoderm now becomes much reduced, so that in Stage F the dorsal ectoderm consists mainly, if not entirely, of a thin layer of nucleated protoplasm derived from the superficial layer of the preceding stage. The hump, however, still persists, retaining the characters it had in Stage E.

With regard to the internal boundary of the ectoderm, in the gastrula stage there was no line of demarcation between it and the endoderm. In Stage B the mesoderm appears, but causes no break in the continuity (Plate VI, fig. 5 *a—f*). In Stages C and D, however, a definite separation occurs, firstly by the appearance of the cavity in the somites, and secondly—and this happens later, in Stage D—by the dorsal and ventral separation of the endoderm from the ectoderm. The endoderm is, however, still continuous with the splanchnic layer of mesoderm, and the ectoderm with the somatic. In the subsequent development this continuity seems to be retained and to be extended in consequence of the growth of the mesoderm over the internal surfaces of the at first uncovered parts of the two primary layers. At any rate I have never been able to see any well-defined boundary between the layers in question, even in the best-preserved embryos, if a careful examination was made with a high power. The defined line drawn in my figures has only an existence with a low power; it is therefore extremely difficult to say whether or no nuclei pass in from the ectoderm to the mesoderm, and often not possible to settle for certain whether a given mass of nuclei belong to the ectoderm or somatic mesoderm. In the later stages (F) this absence of a defined line continues, so that it becomes difficult to decide



whether the external transverse muscles of the body wall are ectodermal or mesodermal.

2. The lateral thickenings, which give rise, amongst other things, to the nervous system, contain during Stages A and B a single layer of long oval nuclei (Plate VI, fig. 5 *b*). They are at first confined to the ectoderm immediately overlying the mesoblastic somites, and constitute on each side a continuous band extending from the pre-oral region, where they are more ventrally placed and continuous with each other across the middle line, to the primitive streak behind. They diverge from one another as they pass backwards, and end in the ectoderm of the primitive streak. During Stages A and B they contain a single layer of oval nuclei, which rapidly increase in number, and become arranged in Stage C in parts in more than one layer. The latter fact is especially conspicuous in the pre-oral portions, i. e. in the portions which will give rise to the cerebral ganglia (Plate VI, fig. 6 *a*).

In Stage D the lateral thickenings have increased considerably in extent, occupying the whole of the sides of the body, and encroaching on the middle region of the body, where in the previous stages they were widely apart, somewhat on the ventral surface (Plate VI, figs. 9, 11), so that the relation to the somites mentioned above (p. 55) is lost. The increase in the number of nuclei is now more marked, and is found to concern chiefly two regions: (*a*) nearly the whole of the pre-oral parts of the lateral thickenings (Plate VI, fig. 14); (*b*) the ventral (inner) portions only in the circumoral and postoral regions (Plate VI, figs. 9, 13). The increase has for its results, as may be seen by reference to the figures, the production of some roundish nuclei lying internally to the oval nuclei. These round internally placed nuclei are much more numerous in Stage E, and eventually give rise to the whole of the cerebral ganglia and ventral nerve-cords. They remain up to the close of Stage E in close connection with the external layer of oval elements, though in some sections there are, in the post-oral region, indications of a commencing separation between them (Plate VII, fig. 23 *a—d*). The manner of separation of



the central nervous system from the superficial ectoderm will be described subsequently.

It is only necessary for me to point out here that in the region of the brain this separation does not occur, as the ectoderm is invaginated, and remains in connection with the nervous tissue throughout life (Pl. VII, fig. 22 *a*, and Pl. VIII, fig. 33).

In Stage *D* a small amount of the so-called punctated tissue appears on the dorsal surface of this rudimentary central nervous system; this tissue, which is earlier and more largely developed in the cerebral rudiments than in the ventral cords, consists of a fine protoplasmic network, which stains but slightly and is almost entirely without nuclei. A similar network exists in the ventral nucleated parts of the nervous system, but is there obscured by the crowded nuclei. At first the whole central nervous system was similarly crowded with nuclei (Plate VI, figs. 15, 16 *a*, &c.), but in Stage *D* the latter began to withdraw from the dorsal part, thus allowing the non-staining protoplasmic network to stand out with great distinctness (Plate VII, figs. 22, 23 *a*, &c.). At the boundary between this white matter and the nuclear mass there are, in Stages *E*, *F*, some nuclei which are somewhat larger than the rest, and more loosely arranged, so that they may be said to lie in the ventral part of the white matter (Plate VIII, figs. 38, 39, &c.). Four such may generally be seen in each section of the ventral cords.

I must now pass to describe the changes of the more dorsal parts of the lateral thickenings in the postoral region. In Stage *D* they contain a single layer of oval nuclei, and become at the same time pushed outwards by the outgrowths of the hinder part of the mesoblastic somites (Plate VI, fig. 9). These outgrowths are arranged in pairs, one pair from each pair of somites, and they constitute the rudiments of the postoral appendages. The first pair to be formed is the pair which will become the jaws; the next pair will form the oral papillæ, and so on in order from before backwards. When the appendages are well established—in Stage *E*—it may be

seen from an inspection of transverse sections that they are special developments of the posterior portion of lateral ridges of ectoderm which extend on each side for the whole length of a somite (Plate VII, figs. 18 *a, b*, 21 *a, l. r.*). Immediately within these ridges there is a thickening of the somatic mesoderm (*m. t.*) which I shall speak of again later, and which is continuous with the thickened mesoderm of the appendage itself. The postoral appendages, therefore, may be described as special developments of longitudinal ridges, which, however, are not continuous up the whole length of the body, but are interrupted at the lines of segmental division. These limb-ridges in Stage E become separated from the appendages and continuous with one another dorsal to the appendages (Plate VIII, fig. 36). They now, therefore, form one continuous ridge on each side of the body, placed just dorsal to the insertion of the appendages. They eventually disappear.

In Stage E the portions of the lateral thickenings dorsal to the line of insertion of the appendages, and the dorsal ectoderm itself undergo a peculiar modification. The ectoderm here becomes thicker, and this increase in thickness is due, mainly, to an increase in the protoplasmic layer, elsewhere of extreme tenuity, on the outer side of the nuclei (Plate VII, fig. 23 *a—d*). This modification, which has already been referred to (p. 54), is seen first, and is always most conspicuous in the region of the seventh (Plate VII, fig. 25) to about the tenth somite, where the nuclei become numerous and arranged in several layers.

There is only one other portion of the postoral ectoderm which needs consideration, viz. the inner portion of the original lateral thickening—the parts which give rise to the nerve-cords.

These are at first perfectly continuous from end to end of the body. They consist, in Stage E, when they first become well marked, of a number of oval nuclei with intermixed round nuclei in the deeper parts (Plate VII, fig. 23 *a—e*). In Stage D they were wide apart, being separated by an area of extremely thin ectoderm (Plate VI, figs. 9—13). The latter, however, soon becomes of less extent (*vide* sections of

Stage E), so that they approach one another until, in Stage F, they meet and coalesce in the middle line (Plate VIII, figs. 38—41). They retain, however, always a trace of their paired origin. In late embryos of Stage F, the nerve-cords separate from them, and they become segmented in such a manner that they persist only between the appendages, the intervening portions having disappeared. In this condition they have been called by Kennel (No. 29) the ventral organs. The ventral organs, as Kennel has already described, persist into the adult, in which they are much more conspicuous in some species than in others. The ventral organs of the jaws and oral papillæ undergo special changes which have already been quite correctly described by Kennel, and which I shall have occasion only to refer to hereafter.

It now only remains for me to describe the changes which take place in the pre-oral portions of the lateral thickenings. I have already stated that these are from the first continuous with one another in front and with the postoral portions behind the mouth, that the internal rounded nuclei appear sooner in them than elsewhere, and in greater numbers. In fact, nearly the whole of the pre-oral lateral thickenings gives rise to the internally placed rounded nuclei (Plate VI, fig. 16 a) which will form ultimately the cerebral ganglia. These rounded nuclei extend, though only in a thin layer, even across the middle line in front of the mouth, in which position they first appear in Stage c (Plate VIII, fig. 28, *com.*), and rapidly increasing in number, remain in connection with the ectoderm until Stage E, when they become detached (Plate VII, fig. 22 a, Plate VIII, fig. 31, *com.*) though the cerebral rudiments themselves are still in connection with the ectoderm. It thus appears that the two cerebral ganglia and their connecting commissure are developed as a single structure from the ectoderm.

The ventral cords, beginning at the level of the jaws, are, as we have seen, continuous developments from the lateral thickenings; and the question arises: Does this continuity extend in front of the jaws to the preoral region, or is there a sharp



separation between the cerebral rudiments and the ventral cords?

There can be no doubt whatever that in *Peripatus capensis* there is no such break at any stage of development. A study of transverse sections of many different embryos from Stages c—e conclusively demonstrates that the ventral nerve-cords, which are developments of the inner portions only of the lateral thickenings, are continuous at all stages of their existence, both before and after their separation from the ectoderm, across the boundary between the first and second somites with the inner portion of the cerebral rudiment, which is a development of the whole surface of the pre-oral part of the lateral thickening. It is true that at first this part of the central nervous system is weaker than the parts in front and behind it, but long before the separation from the ectoderm occurs (Plate VII, fig. 19*b*; Plate VIII, fig. 35, *c.o.n.*), it forms a well-marked cord with a layer of white matter. The whole central nervous system of *Peripatus capensis* develops, therefore, as a continuous structure from the ectoderm, and the independent origin and secondary connection of the cerebral ganglia and ventral chain, which has been asserted for some Arthropoda, e.g. for Spiders by Balfour (No. 19), for Annelida by Salensky (No. 44), *Lumbricus* by Kleinenberg (No. 31), and for Mollusca by various observers, does not hold for *Peripatus*.<sup>1</sup> Balfour held the same view with regard to this point in *Peripatus* (No. 18, p. 337).

I entirely agree with the remarks of Hatschek (No. 28, p. 8) on this subject. He holds, in opposition to Salensky, that the circumoral part of the nervous system in the annelid larvæ which he has investigated, develops from the ectoderm in continuity with the apical ganglion and ventral nerve-cords; and I am strongly inclined to think that a further and closer investigation will show the same fact to hold for other Annelids and Molluscs.

<sup>1</sup> Kennel apparently holds the opposite view on this point. It is difficult to believe that the West Indian *Peripatus* differs in this respect from the Cape species.



**The Cerebral Grooves.**—The cerebral ganglia gradually increase in size (Plates VI, VII, figs. 14, 16 *a*, 19 *a*), and their ventral surface becomes in Stage *e* markedly flattened (Pl. VII, fig. 22 *a*) and then invaginated (Pl. II, fig. 35), so as to form two grooves, which rapidly become narrower and deeper, until in Stage *f* they form two slits, longitudinally arranged, ending blindly in front, but opening behind into the buccal cavity (Plate II, fig. 36, and Plate VIII, fig. 33). Eventually, in old embryos of Stage *f*, they lose their external openings, become reduced in size, and form two vesicles in the ventral portions of the cerebral ganglia. Owing to the relatively greater growth of the latter they appear to form, in the adult, small hollow appendages of the brain (No. 20, Pl. XVII, fig. D, *d*).

The most important features which remain to be described in the development of the preoral part of the central nervous system, is the part which it takes in the formation of two organs—the eyes and the tentacular nerves.

The Eyes arise in Stage *d* as a pair of invaginations of the postero-lateral parts of the cerebral rudiments (Plate II, fig. 29). The two pits so formed are placed immediately in front of the point of origin of the lip-folds from the pre-oral lobes (Plate II, fig. 30). They are at first shallow, but soon become deeper, and eventually (by the end of Stage *e*) constricted off from the surface, so as to form closed vesicles (Plates VI, VII, figs. 16 *a*, 15, 19 *a*, 22 *a*). The eyes, therefore, are nothing more nor less than invaginations of the lateral portions of the rudiments of the cerebral ganglia, and of the surface ectoderm, which gave rise to and covers the latter. Two elements enter into their composition, (*a*) the surface ectoderm with its oval nuclei, and (*b*) the rounded nuclei of the cerebral rudiment. The columnar surface nuclei form the lining of the optic chamber, while the rounded elements which lie behind the inner wall give rise to part of the retina and optic nerve. Figs. 14, 15, 19 *a*, 22, show very clearly the method of development of the optic rudiment. In the later stages the connection between the posterior wall of the optic vesicle and the cerebral ganglion becomes somewhat con-

stricted, but persists throughout life as the optic nerve. The eyes of *Peripatus* are, therefore, as I stated in my original paper (No. 50), cerebral eyes, and are from the very first in connection with the cerebral ganglia.<sup>1</sup>

The tentacular nerves are to be regarded, from their method of development, as forward prolongations of the cerebral ganglia.

In the outgrowths from the pre-oral lobes to form the tentacles the cerebral thickenings, which extend dorsalwards on to the anterior face of the former, participate in such a manner as to form the ventral surface of the developing tentacles (Plate VI, fig. 7). The deep rounded elements of these forward tentacular continuations of the cerebral rudiments eventually separate from the surface ectoderm, and become the tentacular nerves.

The later stage of the cerebral ganglia will be considered subsequently. By the stage reached (Stage F) they are in connection with the walls of the cerebral grooves.

The latter are almost if not entirely constricted off from the surface, and are lined by the ectoderm which gave origin to the cerebral ganglia. Kennel regards this invaginated layer as the homologue of the ventral organs of the postoral region. It differs, however, from the latter in being invaginated. Notwithstanding this, the view seems to me a plausible one.

The cerebral ganglia of *Peripatus* resemble, therefore, in their development and method of removal from the surface, the central nervous system of the Vertebrata, and the cavity of the ventral appendages of the adult brain corresponds<sup>2</sup> with the central canal of the latter.

These cerebral grooves seem a fairly constant feature in Tracheate embryos. They do not, so far as I know, persist into the adult of any other Arthropod, but disappear in the course of development. In these cases their walls are said to become

<sup>1</sup> Kennel states that in the West Indian species the eye arises independently of the brain, and secondarily enters into connection with it. I cannot, however, help thinking that he is mistaken on this point.

<sup>2</sup> By this, of course, I do not mean that the two structures are homologous.

transformed into parts of the supraœsophageal ganglia. Structures of a similar nature are found in other animals. They have been described by Kowalevsky in the embryo of *Dentalium* (No. 32), in which animal the cerebral ganglia are formed from the walls of two invaginations of ectoderm at the apical pole of the body. They persist for some time, and then vanish. In *Sipunculus* Spengel (No. 52) has described a single canal leading from the cerebral ganglion to open at the base of a tentacle. In Nemertines, as is well known, canals opening on the surface penetrate into the cerebral ganglia, and in *Balanoglossus* a single canal traverses part of the central nervous system. Whether these canals leading to this important part of the central nervous system are homologous it is difficult to say. Probably they are not, but are simply analogous, their function being, or having been, in some aquatic ancestor, respiratory. I have already (No. 48) suggested this as the probable genetic explanation of the central canal of the Vertebrate nervous system.

**Summary of the Early Development of Nervous System.**—The lateral thickenings are from their origin continuous from somite to somite. They begin in front of the mouth, where they are connected with one another across the middle line, and they end behind in the ectoderm of the primitive streak.

The rounded elements which give rise to the nervous system are derived from the ventral parts of these thickenings. They are formed first in the pre-oral region, and then in the lateral cords; that is to say, the nervous system at its very first appearance is a continuous structure beginning in front of the mouth, where it is continuous across the middle line, and extending backwards on each side of the mouth.

The portions of these two cords in front of the mouth become the cerebral ganglia, which give rise directly to the eyes and tentacular nerves; the portions around the mouth become the circumoral commissures, while the portions behind the mouth are the rudiments of the ventral nerve-cords of the adult. The ectoderm from which the rounded elements arise remains thickened, and give rise to structures which have been called



by Kennel the ventral organs. The ventral organs are at first placed at a little distance from the middle line. Eventually, however, they approach one another and meet, excepting in the region of the mouth and pre-oral lobes.

On the pre-oral lobes the structures corresponding to the ventral organs of the posterior part of the body become invaginated and separated from the surface in such a manner as to form the linings of the vesicles, which are attached throughout life to the ventral surface of the cerebral ganglia.

3. The Stomodæal and Proctodæal Ingrowths.—At the time when the blastopore is a continuous slit and traversed by strands of anastomosing protoplasm, i. e. during Stage A, the part of the endoderm which is continued into the ectoderm at the lips of the blastopore, resembles, in the small size and number of the vacuoles and the regular shape and arrangement of the nuclei, the ectoderm. In fact it is impossible to say whether this layer is really ectodermal or endodermal. By its position and development it resembles endoderm, by its characters ectoderm.

When the blastopore closes in the middle these cells are left inside and form the median ventral wall of the mesenteron (Plate VI, figs. 5 *b*, 6 *c*, *v. en.*), and eventually assume the characters of endodermal nuclei. At the primitive mouth and anus, however, they still persist as rows of nuclei intervening between undoubted ectoderm and endoderm (Plate VI, fig. 6 *b, d*), and they extend forwards for a short distance, forming the median ventral wall of a portion of the pre-oral enteron (Plate VI, fig. 4, and Plate VIII, fig. 28). It is by the growth of this tissue that the lining of the stomodæum and proctodæum is formed.

The details of the development of these structures will be best treated in the next section dealing with the alimentary canal.

4. The slime-glands arise in Stage E as hollow invaginations of the ectoderm of the oral papillæ (Plate VII, fig. 23 *d*, *s. gl.*). They gradually increase in length and project into the central compartment of the body cavity. Kennel's description of the origin of these organs agrees with my observations.



## THE ENDODERM.

The endoderm during Stage A and earlier stages consists simply of the inner portion of the vacuolated protoplasmic wall of the embryo. Its vacuoles are somewhat larger and its nuclei fewer and more irregular in shape than those in the outer or ectodermal portion. But the two are perfectly continuous (*vide* figures on Plate V). The vacuoles of the layer immediately within the ectodermal nuclei are larger than those in the innermost layer, i. e. in the layer next the gut cavity.

Processes from the endoderm cells project into the enteron and anastomose with each other. This is a well-marked feature in embryos rather younger than Stage A, and indicates the origin of the gut as a vacuole or a concrescence of vacuoles (Plate V, fig. 23).

These processes persist until Stage B at the blastopore, as I have already mentioned in Chapter II (*vide* figs. 24 *b*, 26 *a*, on Plate V). At the hind end of the blastopore they become particularly well developed (Plate V, fig. 25 *a*), so much so that it is impossible to say in which section the blastopore ends and the primitive streak begins. In other words, the blastopore passes quite gradually into the primitive streak. Or again, to put it another way, the primitive streak only differs from the hind end of the blastopore in the fact that the anastomosing protoplasmic strands, which everywhere traverse the blastopore, contain nuclei in the former case, but not in the latter. On this view, in favour of which I may refer to Plate VI, fig. 1, which represents a section through the primitive streak of Stage A, and to Plate V, fig. 25 *a*, which is a section through the hind end of the blastopore, the primitive streak is the hindermost portion of the blastopore.

The nuclei of the endoderm are large, and particularly remarkable for the irregularity of their shape. They do not, excepting those near the lips of the blastopore, ever present the karyokinetic figures characteristic of dividing nuclei; they appear to divide directly. Some of them are much branched

like connective-tissue cells; a feature which is not at all exaggerated in the figures.

The nuclei of the lips of the blastopore, which have already been described as intermediate between ectodermal and endodermal nuclei, constantly present the karyokinetic figures characteristic of dividing nuclei (Plate VI, fig. 3, *d. n.*, and Pl. V, fig. 26 *b*).

During Stages *b* and *c*, the endoderm, though diminishing somewhat in thickness, retains all the characteristics just described.

During Stage *b* the blastopore, which has grown considerably in length, and markedly dumbbell-shaped in surface views closes in its middle portion (Plate II, figs. 23—25). This is effected simply by the approximation and fusion of its lips (Plate VI, fig. 5 *b*). The connection, which has hitherto existed between the latter by the anastomosing strands already mentioned, now becomes closer and they completely unite with one another. The result of their union is that the intermediate nuclei come to lie inside and form a definite part of the endoderm, viz. the ventral endoderm in the median line between the mouth and the anus (Plate VI, fig. 6 *c*). By their fate then these intermediate nuclei are endodermal, and so indeed I think we must regard them, unless we are willing to take the view that the median ventral endoderm of the alimentary canal of *Peripatus* is ectodermal in origin. Up to the close of Stage *c* the endoderm has been in close contact and continuous with the ectoderm, excepting where the mesoblastic somites, which appear in Stage *b*, intervene. In Stage *d*, however, a remarkable change takes place, the endoderm separates ventrally and dorso-laterally from the ectoderm, and there is now a direct connection between the two only along the dorsal middle line (Plate VI, fig. 9). This is soon lost in Stage *e*, and henceforth the endoderm layer is only connected with the ectoderm through the walls and cells of the mesoblastic somites, and at the mouth and anus.

This completes all I have to say about the endoderm till the close of Stage *e*, when it consists of a layer of vacuolated

protoplasm which contains nuclei of irregular shape. But I still have to describe the development of the stomodæum and proctodæum, and the change produced by it in the adjoining parts of the alimentary canal.

The enteron at first reaches the front end of the body. Until the end of Stage c it has a considerable pre-oral extension (Plate VIII, fig. 28). The anterior end of the body now becomes retracted, so that in Stage d the mouth lies at the very front end of the middle ventral line (Plate VIII, fig. 29), though laterally the two pre-oral lobes project for a considerable distance (Plate VIII, fig. 32). The result of this is that the intermediate nuclei, which in Stage c extended forwards from the mouth (Plate VIII, fig. 28), now extend backwards and form the dorsal wall of the developing stomodæum. At the same time the lateral walls have appeared as special developments of the same intermediate nuclei (Plate VIII, fig. 32).

The median ectoderm of the front end of the body so far has been in contact with the front end of the stomodæum (Plate VIII, figs. 29 and 32). It now separates from it (cf. Plate II, figs. 33, 34) and grows forward, so that a space becomes established between the dorsal wall of the stomodæum and the front end of the body (Plate VIII, fig. 31). At the same time the dorsal wall of the stomodæum grows rapidly backwards, while the front end of the enteron maintains its position, or is, perhaps, thrown slightly forward. In this way a blind pocket of the enteron is established, lying on the dorsal side of the stomodæum (Plate VIII, fig. 31, *p.p.*). This anterior blind diverticulum persists for some time (late in Stage f) and then disappears without leaving a trace. It has been observed and described by Kennel.

The stomodæum, the sides and roof of which are first developed (Plate VIII, fig. 32, and Plate VI, fig. 16 *a, b*), soon increases in extent, and by Stage f has acquired a well-developed floor (Plate IX, fig. 49). It is now definitely established, and has a thick lining of oval nuclei and a narrow lumen (Plate VIII, fig. 36). It has also acquired a mesodermal covering from the splanchnic walls of the first and second so-



mites (Plate VIII, fig. 32, and Plate VIII, figs. 14, 16 *a*, &c.). Its further development will be followed subsequently, but I may now state that it becomes the pharynx and œsophagus of the adult.

Behind, the walls of the enteron extend to the hind end of the body below the primitive streak, and the anus not being terminal (Plate II, fig. 25), there is at first a postanal gut. This state of things continues (Plate VIII, figs. 28, 29) until the formation of the proctodæum, which happens when the anus has shifted to the hind end of the body, and the embryo has acquired its full complement of somites (Plate VIII, fig. 30). The proctodæum is due to the growth of the intermediate nuclei. It eventually becomes of considerable extent, acquires a mesodermal investment from the splanchnic walls of the adjoining somites, and finally constitutes the rectum of the adult (Plate IX, fig. 42).

The nuclei of the embryonic endoderm of *Peripatus* are remarkable for being branched and angular. Nuclei of a similar character are found in other animals. Leydig (No. 35) has described branched nuclei in the Malpighian tubules and epithelium of the alimentary canal of Arthropoda, and Balfour (No. 19) speaks of large angular nuclei as occurring in the yolk-segments of *Araneina*. The angular shape is not retained in the adult *Peripatus*.

#### THE MESODERM.

The early stages in the formation of the mesoderm, up to the end of Stage A, have been fully described in Chapter II.

The nuclei of the mesoderm, which arise from the nuclei of the primitive streak, extend laterally and grow forward on each side of the blastopore, at a little distance from it, as the lateral mesoblastic bands. The mesoblastic bands are therefore, primarily at any rate, outgrowths of the lateral portions of the primitive streak nuclei. This is shown clearly by fig. 26 *a*, *b*, *c* of Plate V. In this embryo (Stage A) the



mesoblastic bands (*mb.*) had only a very small extension forwards (five sections in front of the blastopore). They consist of bands of nuclei placed in the vacuolated protoplasm intervening between the ectoderm and endoderm.

The mesoblastic bands gradually acquire a greater extension forwards as the embryo and the blastopore increase in length. They very soon become segmented—before they have reached the level of the front end of the blastopore. This fact is clearly shown by Plate II, figs. 23 and 24. The segments so formed do not at first (Plate II, fig. 23) possess any distinct central cavity around which the nuclei are arranged. By the stage figured in fig. 24, Plate II, in which five mesoblastic somites are present, the cavities have appeared.

The appearances presented by surface views are confirmed by an inspection of sections. I have sections of embryos, in which three solid somites could be made out on each side. Plate VI, fig. 2, represents a transverse section through a stage with one solid somite. The section is slightly oblique and passes through the somite of one side only; on the other side the section passes in front of the mesoderm. Fig. 5 *a—f*, Plate VI, represents sections through an embryo of the stage of fig. 25, Plate II, in which the somites had reached the level of the anterior end of the blastopore. A distinct cavity, around which the nuclei of the somites are arranged, is present in the somites. By the close of Stage B (fig. 25, Plate II) the somites of the anterior pair have reached their permanent position in front of the blastopore. They are separated from one another by the alimentary canal, which at this stage extends in front of the mouth (Plate VI, figs. 4, 6 *a*).

With regard to this development the following questions which can only be settled, if they can be settled at all, by a study of transverse sections, present themselves:—(1) How do the mesoblastic bands grow forward before they have segmented into the somites? and (2) How do the somites, which are established before the bands have reached the front end of the blastopore, reach their final position?

1. Do the bands grow forward independently of surrounding

structures? or do they receive nuclei from the adjacent ectoderm and endoderm? It must be remembered that the first somite is separated from the anterior end of the mesoblastic bands before the latter have reached the level of the middle of the blastopore, so that we are now only concerned with the old embryos of Stage A. After prolonged and careful study of a large number of embryos, I have come to the conclusion that this is a point which it is impossible to settle with certainty by a study of preserved specimens. Still there is a certain amount of evidence, which, on the whole, tends to show that the intermediate nuclei at the lips of the blastopore do contribute to the bands. The evidence depends upon the appearances presented by these nuclei at the lips of the blastopore. These are constantly met with in a state of division, i. e. presenting the figures which are characteristic of dividing nuclei. This is shown clearly in many of my figures, e. g. (Plate V, fig. 26 *b*; and Plate VI, fig. 3). Further, immediately within these intermediate nuclei, and lying between the ectoderm and endoderm, there are often to be seen nuclei, which may fairly be supposed to have been derived by division from the intermediate nuclei. These are present in sections through the young mesoblastic bands (Plate V, fig. 26 *b*), and also in sections in front of the latter (Plate VI, fig. 3, close to *d. n.*); in the former case indicating that the nuclei in question are reinforcing the nuclei of the mesoblastic bands; in the latter that they are laying down the same structures.

2. With regard to the second question, I can only state that the completed somites attain their final position by an alteration in the relative position of the structures in the anterior region of the embryo.

Plate VI, figs. 4, 5 *a—f*, are illustrations of the structure of the embryo at the close of Stage B (Plate II, fig. 25). Fig. 4 is in front of the mouth, and is through the first pair of somites, now pre-oral. Fig. 5 *a* is through the mouth and second pair of somites; fig. 5 *b* between the mouth and anus, through the region in which the blastopore lips have come together and fused; fig. 5 *c* is through the anus; fig. 5 *d, e, f*, behind the

anus through the primitive streak. The somites of this embryo differ from those of the earlier stages only in the fact that they contain a well-marked cavity. Their walls are still in continuous contact with the ectoderm and endoderm respectively. The primitive streak of this stage needs, however, more consideration. In the first place the primitive groove has become much more marked and extends over a greater distance than in the earlier stages (Plate II, fig. 25, and Plate VI, fig. 5 *d-f*). Immediately behind the blastopore the primitive streak consists of but few nuclei, which form a layer placed between the ectoderm and endoderm, and extending laterally as far as the mesoblastic bands. The latter structures here bend in towards the middle line, so that a few sections behind (fig. 5 *e*) they have reached and become indistinguishable from the primitive streak. The primitive streak in this region is much more bulky and consists of a large mass of nuclei. It extends back for about thirty sections behind the blastopore. There can be no doubt that the mesoderm of the developing hind end of the embryo, which now begins to grow forward so as to lie with its ventral side on the ventral side of the anterior part (*vide* Plate II, figs. 26—31), is derived from the continually proliferating cells of the primitive streak. The latter is indeed simply the growing point of the embryo, and in it the three layers of the embryo are united and indistinguishable from one another. It persists until the full complement of somites is obtained and then disappears. Some time before its disappearance it becomes relatively of less extent, and the anus consequently comes to lie nearer the hind end of the body until, at its complete disappearance, the anus has gained its permanent position at the hind end of the body. Plate VI, fig. 6 *d*, illustrates the structure and appearance of the streak during Stage c. The section was taken at the hind end and cuts the embryo, the ventral flexure of which is beginning, at two points, viz. in the region of the primitive streak and in the region of the anus. The later stages of the primitive streak are shown best in longitudinal vertical sections (Plate VII, figs. 28—30).

The large pole-cell of the primitive streak, visible during

Stage A, and in the earlier embryos of Stage B, vanishes later in Stage B. I do not know what becomes of it.

Of the mesoblastic somites during Stage C there is but little to say. They maintain the same relations and structure (Plate VI, fig. 6 *a—d*) as in the preceding stage, that is to say their walls are everywhere in contact with the adjacent ectoderm or endoderm. The cells of the somatic layer are thicker than those of the splanchnic layer. This difference was observable in the previous stages (Plate VI, fig. 5 *a*), and becomes, as we shall see, much more marked in the subsequent stages. During Stage D, somites are still being formed at the hind end from the actively growing tissue of the primitive streak. This stage may be said to mark the close of the formation of new somites, i. e. by Stage E the embryo has acquired its full complement, though the posterior are so small and rudimentary that they are not visible from the exterior.

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## CHAPTER IV.

### THE CHANGES FROM STAGE A TO F (CONTINUED).

#### THE LATER HISTORY OF THE SOMITES AND DEVELOPMENT OF THE BODY CAVITY.

The elucidation of the further changes in the somites, and the development of the body cavity and heart, has presented some difficulties,—difficulties which have very much delayed the publication of my work, but which I am glad to say I have at length completely overcome. It will, I think, be convenient to explain the terms I shall use, and briefly to summarise the results I have obtained, before proceeding to a detailed description.

The somites are obviously comparable to the somites of other animals. It is no less clear that the cavity in them is homologous with the cavities of the somites of other types, e. g. other Arthropoda and Annelida. I propose, therefore, to call the system of somite cavities and its derivatives the *cœlom* or *enterocœle*.

The system of cavities, on the other hand, which arise partly in consequence of the withdrawal of the ectoderm from the endoderm, and partly secondarily in masses of mesoderm, is what in other animals would be called a *pseudocœle*. For this second system of cavities and its derivatives I shall therefore use the words *pseudocœle* or *vascular space*.

My results can be summed up as follows :

1. The adult body cavity comes entirely from *pseudocœle*. The *enterocœle* has no part in its formation.
2. This statement applies also to the heart and pericardium. These are both *pseudocœlic*, and have nothing to do with *enterocœle*.

3. The only products of the enterocœle cavity are:—(a) The nephridia. (b) The generative glands and their ducts.

4. The nephridia do not open either in the embryo or in the adult into the body cavity proper (i.e. in *Peripatus* the pseudocœle), but into a vesicle in each appendage which has hitherto been unnoticed.

These results, when taken in conjunction with the following peculiarities of Arthropod organisation, viz. the feeble development of the somites, the apparent absence of nephridia, the vascular character of the pericardial cavity, and the possession by the heart of lateral ostia opening into the pericardium,<sup>1</sup> will not be without interest to morphologists.

Kennel (No. 29) was the first to point out that the median chamber of the body cavity and the pericardial chamber were not products of the enterocœle; but Kennel erred in supposing that the cavities in the legs and the so-called lateral sinus (No. 29, p. 202) were derived from the somites. In his later memoir he apparently gives up this view so far as the lateral sinus is concerned, but still maintains that a portion of the cœlom becomes broken up by muscles, &c., and persists as the body cavity of the legs. In this, I think, he is mistaken, but it must be borne in mind that he has worked at a different species in which it is possible, though not likely, that the development of the structure in question may be different.

Kennel's observations of the fate of the so-called median divisions of the somites and of the origin of the generative tubes, pericardial cavity, and heart, differ, as will be seen, considerably from mine. His account, however, seems to me to lack precision, and I cannot help thinking, especially when I consider that he has altogether confounded the nephridial vesicles of the adult with the leg body cavity (see below), that he has erred here also.

In my preliminary paper to the Royal Society (No. 50) I also made the mistake of supposing the leg cavities were

<sup>1</sup> This Arthropodan character was first pointed out to me by Professor Lankester. I have never seen attention called to it in any works or memoirs on this subject.

cœlomic, but my account of the generative organs and their ducts was correct. I expressly stated in that paper that I had not succeeded in following the later changes in the somites. My words were as follows :

“So far the development of the somites is quite clear and easy to follow. But the changes by which the dorsal divisions of the somites are converted into their permanent form take place at a late period of development—during November—and are, in consequence of the thinness of the walls, extremely difficult to follow. I have not succeeded entirely in following them. I will content myself, therefore, with making the following statement, of the truth of which I am by no means confident. The dorsal divisions unite with each other transversely and longitudinally, and give rise to a continuous cavity—the pericardial cavity. The portion of this cavity containing the generative cells become separated from the rest as two tubes which form the generative glands and part of their ducts, and come to lie ventral to the pericardium in the central compartment of the body cavity. The external parts of the generative ducts appear to be derived from the modified leg cavity of the anal papillæ.”

With regard to previous observers of the adult anatomy, Balfour—the discoverer of the nephridia—overlooked the small vesicle in the leg cavity into which the funnel of the nephridium opens. This oversight is not to be wondered at in the case of the species (*capensis*) which he worked at, for the vesicle is extremely difficult to see in the adults of *Peripatus capensis*. Gaffron—the discoverer of the pericardial cavity and cardiac ostia—similarly overlooked the vesicle, though it is quite distinct and easy to see in the species—*Peripatus Edwardsii* (?)—which he examined.

#### DESCRIPTION OF THE DEVELOPMENT OF THE MESODERM WITH ITS CAVITIES FROM STAGES D—F.

It will facilitate matters if I begin by describing the development of a particular pair of somites and of the mesodermal structures around them, and I will take for this purpose the third somite of the body (somite of the oral papillæ) as one which is typical of the rest and in which the changes are most easily followed.

During Stage D, at the time when the ectoderm separates from the endoderm, the walls of the dorsal and ventral portions of each somite come together; the cavity is thus obliterated and a single layer of cells<sup>1</sup> lying in close contact with the ectoderm results (cf. Plate VI, figs. 9 and 12, *d. s.*, *v. s.*).

At the same time some cells appear between the somatic wall of the somite and the ectoderm (Plate VI, fig. 10, *me.*). These cells, which are undoubtedly derived from the somatic mesoderm, extend the whole length of the somite. In the anterior part, i. e. in front of the limb outgrowth (Plate VI, fig. 10), they are less numerous than in the region of the latter, i. e. in the posterior part of the somite (Plate VI, fig. 9).

The same arrangement is present in a more advanced state in the later embryos of Stage D (fig. 29, Plate II), cf. Plate VII, fig. 17, *a—d*. Fig. 17 *a*, *me.*, shows the mass of cells in the front part of the somite, anterior to its connection with the somatic mesoderm. The same section also shows the anterior part of the limb-ridge overlying this cell-mass. Fig 17 *b* shows the connection with the mesoderm, while figs. 17 *c* and *d* show this mass in the posterior part of the somite in the region of the limb outgrowth. In the posterior part of the somite some of the cells of this mass project into the cavity of the somite in such a manner as to tend to separate the limb portion from the portion in the body, and at the same time a cavity appears amongst the cells at the base of this rudimentary septum (fig. 17 *d*, *b. lat.*). Both these latter features are more clearly shown at *sep.* and *b. lat.* in Plate VI, fig. 13.

In a slightly more advanced stage (intermediate between D and E) the cells of this parietal mass, as I may call it, are more numerous, and the contained cavity—*b. lat.*—extends forwards to the anterior part of the somite (fig. 21 *a*, *me.*, *b. lat.*); while in the posterior part of the somite, in the region of the limb outgrowth, the rudimentary septum has become more marked

<sup>1</sup> It is difficult to say whether these layers of cells arise in this manner or as outgrowths from the dorsal and ventral corners of the somites.



(fig. 21 *c*, *sep.*), but the median portion of the cœlom still communicates with the lateral or appendicular portion (Plate VII, fig. 21 *c*). The latter (*l. s.* 3) has developed a ventral outgrowth, which lies along the outer side of the nerve-cord, and reaches the ectoderm. The ectoderm becomes slightly indented at the point of contact, where a perforation is soon formed.

In the next stage (E) four changes are noticeable (Plate VII, fig. 23 *a—c*) :

(1) The dorsal or median part of the somite has extended itself dorsalwards (fig. 23 *a*). At the same time it does not extend so far backwards as the lateral part (i. e. the part in the appendage), so that the latter is overlapped by the median portion of the somite behind (Plate VI, fig. 23 *d*, *l. s.* 3, *s.* 4). (It must be remembered in this connection that the outgrowths into the developing appendage takes place at the hinder part of the somite.)

(2) The space (*b. lat.*) in the parietal mass of mesoderm (*m. t.*) has much increased (fig. 23 *a*), and has, at the same time, become partly divided by a tongue of cells, which eventually give rise to the muscles of the posterior internal projection of the jaw.

(3) There exists a short, anteriorly directed, blind diverticulum (or, may be, constricted-off groove), in the form of a tube, from the neck connecting the median portion with the lateral portion of the somite (figs. 23 *b*, *c*, *a. v.*, and *l. s.* 3).

(4) The lateral portion of the somite has acquired an opening to the exterior (fig. 23 *e*). This happened in a slightly younger embryo. The opening is already covered over by the lip (*L.*), which is rapidly growing backwards (cf. Plate II, fig. 35; embryo with commencing cerebral grooves).

Briefly to recapitulate, the structure of the third somite at this stage is as follows:—In front it is dorsally placed and overlaps the second somite; its middle portion slopes ventralwards and communicates with the posterior part, which is contained in the limb, and is peculiarly bent (fig. 23 *c—e*), and opens to the exterior. The middle portion further sends a

narrow diverticulum forwards for a short distance (fig. 23 *b*, *a. v.*). The parietal mass of cells is larger than in the last stage, and contains several cavities, which are not derived from the coelom, but arise independently in it.

As in the earlier stages, there is a sheet of cells closely applied to the ectoderm, and extending from the dorsal end of the somite to the middle dorsal line (*d. s.*), and from the ventral corner (*v. s.*) along the parietal mass of mesoderm and the inner surface of the nerve-cord to the ventral ectoderm. Further, the endoderm has entirely separated from the ectoderm, so that two large spaces are left, the one dorsal (*b. h.*), and the other ventral to the gut (*b. bc.*). These spaces contain a few scattered, more or less branched cells, which appear to be derived from the splanchnic walls of the somites, and are therefore probably mesodermal in nature.

There are therefore four distinct systems of spaces present in the embryo at this stage (E) :

1. The cavity of the gut derived from a vacuolation of the endoderm mass of the gastrula stage.

2. The cavities of the somites, derived from a vacuolation of the protoplasm of the mesodermal bands.

3. The spaces which appear independently of the other spaces in the parietal masses derived from the somatic walls of the somites.

4. The spaces formed by the separation of the endoderm from the dorsal and ventral ectoderm, and derived in all probability from the vacuoles found in a corresponding position in the earlier stages (Plate V, fig. 24 *a—d*). These latter spaces are comparable with blastocœle spaces of other embryos, so called because they present the relations of the segmentation cavity of the earlier stages. Such a name is, however, obviously out of place here, inasmuch as the segmentation cavity is never present.

In the next stage (F) the dorsal division of the somite has entirely separated from the ventral, so that the two parts may be considered separately.

The ventral division of the third somite presents the

same parts as in the previous stage. These were, it will be remembered, (1) what I may call a vesicular internal part, extending to the hind end of the appendage and forwards as an anterior diverticulum, and opening into (2) a tubular part, projecting ventrally and opening to the exterior.

In Stage *r* the vesicular internal part (Plate VIII, figs. 36, 37, *l.s.v.* 3) has not only lost its connection with the dorsal (median) part of the somite, but its peripheral part—viz. that in the appendage—has become largely obliterated by the increase in the thickness of its mesodermal walls, and by the growth of the slime-gland rudiment. At the same time the tubular part has become longer and more twisted (figs. 37, 38, *l.st.* 3), and its external opening covered up by the lips, which have met on the ventral surface (Plate II, fig. 36). The tubular part, therefore, no longer opens freely, but into the posterior part of the buccal chamber.

I will now describe more in detail the structure of the two parts during Stage *F*.

The inner walls of the internal vesicle retain (Plate VIII, figs. 36, 37) the character presented by the walls of the anterior diverticulum of the previous stage (*a.v.* Plate VII, fig. 23 *b*); i. e. the nuclei are relatively far apart, and separated by a slightly staining protoplasm. The outer wall, on the other hand, is reduced to a thin layer.

The tubular portion I shall now call the nephridium. Its opening into the vesicle, shown in fig. 38, is a well-defined structure, which I shall call the funnel of the nephridium. The external opening of the nephridium (fig. 37) is anterior to the funnel. The course of the tube at this stage will be understood by an inspection of figs. 37, 38, 38 *a*. It will be observed from these that the nephridium—the part marked *l.s.t.* 3 in fig. 38—projects back as a tube (fig. 38 *a*, *l.s.t.* 3 = *sal. gl.*) which ends blindly. This backwardly projecting part gains an enormous extension in the later stages, and is known in the adult as the salivary gland.

Kennel, who has correctly recognised the nephridial nature of the salivary gland, has made what I cannot but



regard as one or two blunders in his description of its development.

He says (No. 30, p. 38), "Von allen Theilen der früheren Segmentblase behält nur der 3. Abschnitt, die blindsackartige Ausstülpung, ihren Charakter, indem dort die Zellen als Epithel angeordnet sich erhalten; er wird zum Trichter des Segmentalorgans." Again, on p. 45, "Man findet ihn (segmental trichter of salivary gland) an seiner alten Stelle, allenfalls ein wenig weiter nach hinten verschoben, als kurzen Blindsac, welcher von seiner Ansatzstelle aus schräg nach vorn dicht am eigentlichen Kanal der Speicheldrüse hin verläuft, *nun aber nicht mehr mit Raumen des Lateral sinus communicirt, sondern blind geschlossen ist*" (my italics).

Combining these passages with a statement on p. 38 as to the breaking up of the Segmentblase of the oral papilla, it seems clear that Kennel imagines; (1) that the third somite does not divide into a median and lateral part (though it does so in other somites). (2) That the somite itself breaks up entirely into a system of spaces, of which the lateral sinus is part. This is implied by the first of the above quotations, and the italicised parts of the second. It is also definitely stated on p. 176 of Th. 1 (No. 29) in the following words: "Letzere (i.e. Segmentalhohle) werden später gänzlich in den Lateral sinus und die Höhlung der Füßchen umgewandelt und geben den Hohlorganen daselbst, besonders den Segmentalorganen z. Th. der Ursprung." (3) That the funnel of the salivary gland becomes closed and persists in life as a vesicle. (4) (from other statements on p. 39) that the funnel of the other nephridia are open throughout life into the broken-up space of the foot (or lateral sinus?).

I admit it is rather difficult to make out his exact meaning, his account being somewhat confused and diffuse. But I think I am right in supposing that he maintains in the paper referred to the above four positions. Well, accepting his idea that the later stages resemble one another in the two species, I have little hesitation in saying that he has erred in each particular. The third somite does divide into two parts. The



ventral part does not break up into spaces, nor does it become traversed by muscles and connective tissue, but persists through life as a vesicle with an epithelial lining. The lateral sinus has nothing to do with the *cœlom*, but comes from the space marked *b. lat.* in my sections. The funnel of the nephridium opens always into the lateral part of the somite, of which, indeed, it is a part; and does not become blindly closed. The funnels of the other nephridia do not open into the space of the feet, but into the lateral division of their proper somites exactly as do the salivary glands.

Kennel further maintains that the funnel only of the adult nephridium is mesodermal. I cannot accept this; it is an altogether fanciful view. It may be true, but it is a point quite impossible to settle by sections. With regard to it, I have only to say that the ectodermal ingrowth at the opening of the nephridium is extremely inconspicuous, and that at the early stage, immediately before and after the establishment of the external opening, an ectodermal part such as Kennel describes can only be made out with difficulty.

The dorsal division of the third somite separates from the ventral in an embryo slightly older than that from which series fig. 23, Plate VII was taken, viz. one in which the cerebral grooves were slightly more advanced than in fig. 22, but not so much developed as in fig. 33, Plate VIII. After its separation, it becomes much reduced in size (fig. 36, *d. s.* 3), then still smaller (Plate IX, fig. 45, *d. s.*), and finally vanishes (fig. 46, *d. s.*).

This completes what I have to say about the third somite up till Stage F, by which time the adult condition of the parts is practically attained. The remaining somites conform, on the whole, to the type described. They do, however, present certain differences, of which, perhaps, the most important are found in the posterior part of the body. In the posterior somites the dorsal divisions do not become obliterated, but persist and give rise to the generative glands (Plates VIII, IX, figs. 41, 43, *d. s.* = *gen. o.*). It will be more convenient, however, to defer the detailed consideration of this and other peculiar features of the remaining somites until after the

description of the changes by which the adult body cavity, pericardial cavity, and heart are formed.

#### THE BODY CAVITY AND VASCULAR SYSTEM.

I have already described the first appearance of the body cavity. It arises in Stage D as a space between the dorsal ectoderm and the endoderm (Plate VI, fig. 13 *b. h.*), and between the ventral ectoderm and the endoderm (*b. bc.*). There also appears at the same stage a space in the parietal thickening of the walls of the somites (Plate VI, fig. 13, *b. lat.*). In later embryos of Stage D (Plate VII, figs. 17*a—d*), these spaces are all more marked, and cells—apparently amœboid wanderers from the walls of the somites—have made their appearance in the two former (Plate VII, fig. 17 *a—d.*). These cells apply themselves to the ectodermal and endodermal walls of the chambers in which they are contained, and so form the foundation of the mesodermic investment by which the body cavity of the adult is lined. In the next stage the cavities *b. h.*, *b. bc.*, remain unchanged; but the cavities in the parietal thickenings become definitely established (Plate VII, fig. 21 *a—c*, *b. lat.*). The latter at this stage appear to be segmentally arranged; each one beginning at the anterior end of a somite, and extending backwards to the level of the appendage, in the mesoderm thickening of which it is lost. They are bounded internally by the septum which runs from the ventral border of the somites along the inner side of the nerve-cord to the ventral body wall, and externally by a mass of mesoderm cells which project into what I have called the limb-ridge (Plate VII, fig. 21 *a, l. r.*). In the next stage (Stage E, Plate VII, figs. 23 *a—c*), the two median cavities, *b. h.* and *b. bc.*, present but little alteration, excepting that the dorsal one *b. h.* has been encroached upon by the dorsal extension of the median division of the somite.

The successive lateral spaces have now become continuous, extending through the region of the appendage immediately within the septum (*v. s.*). This is shown in Plate VII,

fig. 23 *c—e*, and more clearly by Plate VII, fig. 25. (The tongue of cells in this space in figs. 23 *a, b*, I shall refer to later in describing the jaw somite.)

Before proceeding, I may mention the fate of the three divisions of the pseudocœle or permanent body cavity which have so far appeared. The dorsal median cavity (*b. h.*), which is from the first a continuous space, begins at the very front end of the body (Plate VII, fig. 22 *a, b. h.*) and extends backwards as far as the ectoderm has separated from the endoderm. It eventually reaches the hind end of the body, and becomes, i. e. all of it, except its very front and hind ends, the heart. The ventral (*b. bc.*), which extends forwards as far as the mouth (Plate VIII, fig. 31), will form the ventral portion of the median chamber of the body cavity of the adult. The lateral cavity, which is at first not a continuous cavity, but eventually becomes so, gives rise in the adult to the lateral chamber of the body cavity (lateral sinus), which contains the nerve-cord and salivary gland.

In Stage *E*, two new cavities appear amongst the nuclei of the ventral corners of the somites (Plate VII, fig. 25, *b. pc.* and *b. bc'*). They are first seen at about the level of the seventh somite, and soon (in Stage *F*) increase in size and extend forwards to the level of the jaw somite, and backwards, eventually reaching the hind end of the body. Plate VIII, fig. 39, shows the typical arrangement of these two additional cavities in Stage *F*. The dorsal of them (*b. pc.*) has extended dorsalwards as far as the median dorsal pseudocœle or rudimentary heart (*b. h.*), which has in this stage become much smaller. The ventral one (*b. bc'*) also has extended dorsalwards as far as the ventral wall of the much reduced somite (*d. s.*). The somite, which in the previous stage extended ventrally as far as the dorsal insertion of the septum (*v. s.*) which separates the lateral chamber (*b. lat.*) from the ventral division of the median pseudocœle (*b. bc.*) (*vide* Plate VII, figs. 23 *e*, 24) has now shrunk, and its space is occupied by the ventral of the two new cavities (*b. bc'*). This latter chamber, therefore, is bounded dorsally by the ventral wall of *b. pc* and of the somite, internally by the splanchnic



mesoderm of the gut wall, and ventrally by a septum separating it from the ventral division of the median pseudocœle (*b. bc.*).

At the hind end of the same embryo the same relations are visible but in a less developed state. Here (Plate VIII, fig. 41) the somites are almost in contact in the middle dorsal line, the heart space (*b. h.*) being very rudimentary. The dorsal divisions of the somites (*d. s.*) themselves are still well-developed structures with the generative nuclei in their floors. The two new chambers (*b. pc.*, *b. bc'*) are present, but in a rudimentary form. It is by looking through a series of sections of an embryo of this age, such a series as that from which figs. 33—41 were selected, and comparing them with the previous stage, that it is possible to settle conclusively the fact that in figs. 38 and 39 the space marked *d. s.* and *s. 4* is the reduced somite—it can be followed backwards, gradually enlarging in successive segments, until at the hind end of the body (in figs. 41, 42) it has exactly the relations of the dorsal division of the somite of the earlier stage—and that the spaces marked *b. pc.* and *b. bc'* are new formations in the walls of the dorsal divisions of the somites and have nothing to do with the true enterocœle or cavities of the somites. They, like the spaces *b. h.* and *b. bc*, are, from the first, continuous structures.

The determination of the relations of these cavities in successive stages has been one of considerable difficulty, for this reason, that the dorsal wall of the body often contracts at the death of the animal and obliterates all traces of the complex system of dorsal cavities. They then present merely the appearance, which has been seen by Kennel and has led him into error, of being an irregular system of spaces in the dorsal mesoderm.

Kennel's description of the origin of the heart and pericardium from an irregular system of spaces in the dorsal mesoderm, derived from the broken-up dorsal divisions of the somites, is quite erroneous.

It is easy to see the arrangements which I have described, if embryos be used in which the dorsal ectoderm has not contracted.



Corrosive sublimate solution with a few drops of acetic, or Perenyi's fluid, or 70 per cent. spirit, seem to be the best reagents for obtaining this result, though their action is by no means certain.

With regard to the fate of the two new cavities the dorsal of them (*b. pc.*) becomes the pericardium (Plate IX, figs. 45, 46); the ventral (*b. bc'*.) enlarges, and by the withdrawal of the gut from the ventral wall of the dorsal division of the somite—which aborts, it will be remembered, in the anterior region (Plate IX, fig. 46) but gives rise to the generative organs in the posterior (Plate IX, fig. 43)—becomes continuous with its fellow. It remains for some time separated from the ventral median chamber (*b. bc.*) by the septum, which results from its method of origin. This septum eventually—Stage g—breaks down, and the cavity *b. bc'*. becomes continuous with *b. bc.*, and the two form one chamber, the median chamber of the definite body cavity of the adult.

I have now described the origin of all the parts of the adult body cavity except those in the legs. These arise in Stage f as spaces in the thickened mesoderm of the appendages (Plate IX, figs. 52, 53, *b. app*).

From the above account it is perfectly clear that, so far as its embryonic development is concerned, the body cavity of *Peripatus* has, as I stated at the outset, nothing to do with the coelom. It is a pseudocœle, a space which arises secondarily, i. e. subsequently to the coelom, partly in the mesoderm masses produced from the walls of the somites and partly as spaces between the ectoderm and endoderm (cf. the vacuoles in the same position in the gastrula stage), which soon become lined by mesoderm cells from the somites. The heart has an origin identically similar to that of the ventral part of the median chamber of the body cavity. The whole system is probably in communication and functions as a vascular space of which the heart is a specially marked off and contractile tract. The body cavity and pericardium of *Peripatus*, if comparable with anything in Annelida or Mollusca, must be looked upon as homologous with the vascular system. The peri-

cardium of a Mollusc is, I think (but to these points I shall return later), from its development (Ziegler, No. 53) an enterocœle, and as such has no communication—in this respect resembling the remains of the enterocœle of *Peripatus*—with the pseudocœle represented by the heart and vascular system and spaces. The chief difference, I take it, between the pseudocœle (body cavity, pericardium, and heart) of *Peripatus* and the pseudocœle (vascular system and vascular spaces) of a Mollusc is that the latter is usually largely broken up by anastomosing strands of muscle and connective tissue, while in *Peripatus* the same space is, except in the legs, a fairly continuous and unbroken system.

If the above suggestions are correct, and if at the same time the body cavity and heart of other Arthropoda develop in the same manner as in *Peripatus* (I shall examine this question later), then that peculiar Arthropod feature, viz. the paired ostia leading from the heart into the pericardium, receives a morphological explanation.

#### FURTHER ACCOUNT OF THE DEVELOPMENT OF THE SOMITES.

After the foregoing description the various parts of the figures will be intelligible, and I may proceed to give an account of the changes which take place in the other somites. In doing this I shall refer to the changes in the mesodermic tissue generally. The somites, with regard to their development as far as Stage F, may be grouped under six heads:—

1. The somites of the pre-oral lobes, or first pair.
2. The somites of the jaws, or second pair.
3. The somites of oral papillæ, or third pair.
4. The somites of legs 1—17, or fourth to twentieth pair.
5. The somites of the anal papillæ, or twenty-first pair.
6. The rudimentary somites behind the twenty-first.

The heading 4 will have to be further subdivided according as the dorsal divisions contain generative cells or not.

The Somites of the First Pair (somites of pre-oral or an-

tennal segment) take up a position in front of and at the sides of the mouth by the end of Stage B. This position they maintain during the whole of development. Their splanchnic walls are, at first, in close contact with the endoderm of the anterior part of the alimentary canal, and afterwards with the ectoderm of the stomodæum when that is formed (Plate VI, fig. 8). They grow forward into the antennæ when the latter appear in Stage D, so that the bases of the antennæ are hollow (Plate VI, fig. 7). Soon—in old embryos of Stage D (Plate II, fig. 29)—the cells of that portion of their inner wall which adjoins the ingrown ectoderm, proliferate, and form a mass of cells (Plate VII, figs. 16 *a*, 19 *b*, *ph. m.*) which ultimately give rise to part of the musculature of the pharyngeal wall and tongue.

In Stage E, or possibly late in Stage D, the wall of the posterior external corner of the somite becomes markedly thickened (Plate VII, fig. 19 *b*, *S. o. 1*) and pushed out ventrally into a short pouch. In the later embryos of Stage E, and in young embryos of Stage F, this pouch, which is placed immediately behind the eye and at the level of the origin of the lip from the pre-oral somite, forms a distinct tube lying along the outer side of the nerve-cord (hind end of brain or beginning of ventral cord), and reaching to and fusing with the ventral ectoderm (Plate VII, fig. 22 *b*, *S. o. 1*) immediately in front of the jaw. So far as I can make out, an actual perforation is never formed at the point of contact. The tube persists until the later period of Stage F, being found in embryos in which the cerebral grooves are partly closed (Plate IX, fig. 50, *S. o. 1*). It then vanishes without leaving a trace.

There can, I think, be but little doubt that this structure is the rudimentary nephridium of the somite. It presents exactly the same relations as do the nephridia of posterior somites; it is a development of the posterior, external, ventral corner of the somite; is closely applied to the outer border of the central nervous system, where it fuses with the ventral ectoderm; and, as we shall see in a moment, the part of the somite into which it opens becomes separated from the remainder. With regard to



the somite itself, it becomes much reduced in size in Stage E, being encroached upon by the rapidly growing cerebral rudiments (Plate VII, fig. 22 *a*). In Stage F, in consequence of the same process, combined with the great development of the cerebral grooves, the first somite becomes much flattened out (Plate VIII, fig. 33). It lies immediately over the white matter of the posterior lobes of the brain, and becomes divided into two parts posteriorly, viz. an external portion placed close to and immediately dorsal to the eye, and an internal or median portion (Plate IX, fig. 51, *S. 1*). The external portion, the walls of which are thicker than those of the median, is continuous with the rudimentary nephridial tube, of which indeed it forms the dorsal end.

The first somite, therefore, behaves exactly as do the posterior somites. It becomes divided into two parts—a median part and a lateral part. The latter sends out a ventral diverticulum, which hugs the outer side of the nerve-cord and fuses with, if it does not open through, the ventral ectoderm.

Kennel has seen the rudimentary nephridium, but he has not appreciated its significance or made out its exact relations to the lateral division of the somite on the one hand and the ventral ectoderm on the other. I should mention that by the time the lateral division of the somite has completely separated from the median, the nephridial tube has nearly vanished. This fact may account for Kennel's omission to notice the connection between the two structures. The suggestion by the same author (No. 30, p. 49) that the eye may possibly be derived from the ectodermal part of the lost nephridium of the first somite, loses, after the discovery of the actual nephridium, any plausibility which it might at first sight have appeared to possess. It is obvious that the nephridium which possesses a rudiment of an external opening behind and ventral to the eye, and within the lip, can have nothing to do with the eye which is derived from the side of the cerebral rudiment.

The Somites of the Second Pair (somites of the segment of the jaws) come to occupy in Stage B their permanent position at the sides of the mouth. In Stage D (the endoderm has



separated from the ectoderm ventrally and on each side of the dorsal line, fig. 9) the rudiment of the jaw is laid down, and the somite is prolonged into it. (Plate VI, fig. 9, which, however, is through the oral papilla, represents quite accurately a section through the jaws at this stage.) The somatic wall of the somite becomes considerably thickened, particularly the ventral portion of it. This is very marked in Stage E (fig. 20, *m. t.*). The somite of the jaw segment is further in Stage E overlapped on the dorsal side by the somite behind (fig. 20). By the close of Stage E (stage of fig. 35, Plate II) the portion of the cavity of the somite contained in the jaw has become almost obliterated by the growth of the cells above mentioned. The median portion persists for some time, and furnishes, from its splanchnic wall, cells which apply themselves to the developing stomodæum and assist in forming the pharyngeal and œsophageal musculature.

The median division of the jaw somite, which has from an early period a much less longitudinal extension than the median divisions of the other somites, coalesces in Stage F with the median division of the third somite.

The walls of the ventral portion of the somite, which entirely fill up the jaw, form the muscles of the jaw and are prolonged backwards in the lateral compartment<sup>1</sup> of the body cavity as the tongue of cells, which has been already referred to and is shown in Plate VII, fig. 23 *a—c*, at *m. l.*

In the following Stage (F) the hind end of the jaws becomes enclosed by folds of the dorso-lateral walls of the buccal cavity and constitutes the rudiment (Plate VIII, fig. 36, *le.*) of the internal backward continuation of the inner blade—the so-called lever of the jaw, which is so marked a feature in the adult. The further history of this structure, as well as that of the tongue of cells, which have been already described for Stage E and are shown in sections of Stage F at *m. l.*, Plate VIII, figs. 36—39, will be described later.

I have not been able to see any trace of even the rudiment

<sup>1</sup> The posterior end of this tongue of cells lies in the central compartment of the body cavity.

of a nephridium of the jaw somite, unless, as Kennel has suggested, the internal prolongation of the jaw be regarded as such.

**The Somites of the Fourth to the Fifteenth Pairs**, i. e. of the first to the twelfth legs, may be taken together. The development is essentially the same for all, and until Stage *r* almost exactly the same. The description of the changes of any one of them will therefore serve for all. Like the other parts of the body, they develop in order from before backwards. The dates given in the description below will refer to the anterior somites.

The changes during Stage *D* are similar to those of the third somite, and the figures 10—12, Plate VI, which were used to illustrate my description of the latter during Stage *D*, are really representations of these posterior somites. As a result of these changes the thickening of the somatic wall, the leg diverticulum, and the rudimentary septum, which partly separates the latter from the rest of the somites, are established. In Stage *E*, the somite has become divided into two parts by the completion of the septum,—into an anterior part placed dorsally (fig. 24, *S.* 4) and a posterior part with a very small lumen contained in the leg (Plate VII, fig. 25 *l. s.* 7). These two portions do not overlap, as might be imagined from the earlier stage seen in figs.<sup>1</sup> 13 or 21 *c*, in which the septum is incomplete, the part of the somite in the body on a level with the leg having disappeared. The spaces in the parietal mass of mesoderm, the origin and history of which has already been described, have increased largely in size (fig. 25) and might easily be mistaken for a portion of the true coelom. It must be carefully borne in mind—as I have already pointed out—that these spaces are, so far as their development in this embryo is concerned, quite distinct from the cavity of the somites, which I regard as the true coelom. I may, however, draw attention to the fact that the two sets of spaces arise in

<sup>1</sup> These figures were not taken from the parts here referred to, but inasmuch as they precisely resemble in all particulars sections from these parts, they can be used as illustrations of the text.

essentially the same manner, but not at the same stage; the cœlomic spaces arise as vacuoles in the multinucleated bodies called mesoblastic somites, while the parietal spaces arise later as the result of the vacuolation of multinucleated masses derived from the walls of the somites.

The development so far has only differed from that of the third somite in the much earlier separation of the median from the lateral portion of the somite.

In Stage E, the cavity of the lateral portions of the somites becomes extremely reduced in size, in consequence of the enormous thickening of their mesodermal walls (Plate VII, fig. 25, *l. s.* 7), and at the same time confined to the base of the appendage, the whole of the distal part of the latter being occupied by a mass of mesoderm cells.

By the end of Stage E, the cœlomic space of the fourth leg (seventh segment) has acquired an opening to the exterior in nearly the same position as the opening of the third somite, i. e. immediately external to the nerve-cord, and by the same process, viz. a ventral outgrowth from the cœlom, which meets and fuses with the ectoderm (Plate VII, fig. 25). The same process takes place in the three preceding legs (legs 1—3), I think, a little later. If this is so, we have an exception to the prevailing rule of development from before backwards. However this may be, the three preceding somites obviously possess their opening at a slightly later stage (early embryo of Stage F, Plate VIII, fig. 40, *l. s. v.* 6<sup>1</sup>). I should mention that even at this early stage the external openings of somites 7 and 8 have not the same position as in the case of the other legs, but are nearer the periphery of the limb (cf. Plate VII, fig. 25, *o. s.* 7, with Plate VIII, fig. 40, *o. n.* 6).

To sum up, at the beginning of Stage F the lateral portions of the anterior somites are small spaces in the base of the legs with a ventral prolongation which lies along the outer edge of, and, except in the case of legs 4 and 5, opens to the exterior immediately outside the nerve-cord. In the case of these

<sup>1</sup> The apparent absence of a lumen in the passage in this figure is due to the contraction of the specimen.



legs, the opening is a little removed from the nerve-cord and placed on the ventral surface of the leg itself.

At the end of Stage F an important change takes place: the pseudocœle or body cavity of the leg makes its appearance. It arises simply as a space in the mass of mesoderm which occupies the periphery of the appendage (Plate IX, figs. 52, 53 *a*, *b*, *b.app*). The space almost at once becomes much larger and more conspicuous than the lateral compartment of the cœlom, the outer wall of which—i. e. the wall which separates it from the new cavity—is extremely thin and delicate. So thin and delicate indeed, and so sudden the appearance of the leg pseudocœle, that I was for a long time inclined to the opinion that the latter was derived from a part of the lateral compartment of the cœlom. I have, however, convinced myself, by prolonged and careful study of my sections, that this is not the case, but that the pseudocœle of the leg, both in its origin and subsequent history, has nothing to do with, and is entirely separate from, the lateral or nephridial compartment of the cœlom. The extreme tenuity of the outer wall of the lateral cœlom of the legs is shared by the same structure in the oral papillæ (third somite) (*vide* figs. 38, 38 *a*, *l.s.v.3*, Plate VIII, and description above, p. 79).

By the close of Stage F we can distinguish, as in the case of somite 3, two parts in the lateral compartments of the somites, viz. (1) an internal vesicular part, with an internal and dorsal wall in which the nuclei are far apart and separated by a relatively large amount of little staining protoplasm, and an external wall of considerable tenuity separating it from the secondarily developed body cavity of the leg; and (2) a tubular part which leads ventrally to the external opening; and even in this stage, except in the case of the first three legs (somites iv—vi), has begun to become convoluted.

The tubular part, which in the case of the first three legs remains straight even in the adult, becomes the structure which was first described by Balfour (excepting (?) Saenger, whose paper I cannot procure) and called by him the nephridium; while the internal vesicular part, which persists through-



out life as a vesicle lying in the leg compartment of the body cavity (pseudocœle) and receiving the internal so-called funnel of the nephridium, has hitherto escaped notice.

The fate of the median compartments of the cœlom of the jaws, oral papillæ, and legs 1—15, I have already described. Except in the case of the second and third somites, in which they coalesce in Stage r, they retain their segmentation until their disappearance. This takes place in Stage r first at the level of about the fifth leg, proceeding backwards and forwards. It is preceded by the diminution in size of the cavity (Plate IX, fig. 45), and the development of the pericardium.

An indication of the somites remains for a short time as a thickening in the floor of the pericardium, with which thickening the ventral wall of the heart is fused (Plate IX, fig. 46, *d. s.*). The floor of the pericardium soon, however, separates from the ventral wall of the heart, so that the two halves of the pericardial cavity become continuous. At the same time the dorsal wall of the heart separates from the dorsal body wall, and the heart then forms a tube lying quite freely in the pericardium. The cardiac ostia seem first to appear in Stage r, and are confined in the *Cape Peripatus*, at any rate, to the posterior part of the heart.

The Development of Somites 16—20 differs from that just described only in so far as concerns the median divisions. The lateral divisions proceed in exactly the same way as in the anterior somites. The median divisions, however, contain in their splanchnic walls the germinal nuclei, and persist throughout life as the generative tubes. Their development therefore requires a special description.

#### THE GENERATIVE ORGANS.

During Stage d a number of especially large (as large as the largest of the ordinary endoderm nuclei), round, granular nuclei appear in clusters in the dorsal endoderm of the hind end of the body. Their anterior limit is the sixteenth somite.

They are not therefore seen until the sixteenth somite is formed. When they first appear they are crowded together in a mass in the endoderm at the hind end of the body; but they soon begin to acquire a relation to the cells of the splanchnic walls of the posterior somites. Some of them pass to the surface of the endoderm and project into the somites, pushing the mesoderm cells before them (Plate VIII, figs. 26 and 27, *gen.*). I think there can be no doubt that they give rise to the nuclei of the sexual cells of the adult, and I propose to call them the germinal nuclei. With regard to their disposition, I may give the following details:—In an embryo with eighteen somites they were present in the region of the last three, viz. of the sixteenth, seventeenth, and eighteenth. They were placed in the endoderm near the layer of splanchnic mesoderm, but they did not project, except in one or two cases, into the cavity of the somite.

In an embryo with twenty-one somites these nuclei were present in the region of the sixteenth to the twentieth somite inclusive. They were found in groups in the dorsal endoderm, and a considerable number of them projected into the somites, or, in other words, had migrated from the endoderm into the splanchnic mesoderm (Plate VII, fig. 26).

The same features were presented by an older embryo of Stage E, with the full number of somites. Plate VII, fig. 27, represents a section through the seventeenth somite of such an embryo, and shows very clearly the relations which these nuclei acquire to the splanchnic mesoderm.

The cells of the latter form capsules surrounding the germinal nuclei, which possess but a very delicate (with difficulty visible) protoplasmic investment of their own. By the close of Stage E these germinal nuclei are present in the region of the sixteenth to the twentieth somite inclusive, lying partly in groups in the dorsal endoderm and partly in the splanchnic mesoderm.

They are of the same size as the larger of the ordinary endodermal nuclei— $\cdot 014$  mm. in diameter. They differ, however, from the latter in their evenly-rounded form, the outline

being perfectly smooth, and in the fact that they lie together in groups of three or more.

With regard to their origin, they come, as do all the tissues of the hind end of the body, from the primitive streak; and though there are in the primitive streak in Stage c large round nuclei of their aspect, it is not until Stage d that they can be distinguished in the endoderm with the above-mentioned characteristics.

The median divisions of the somites in the generative region remain continuous with the lateral (nephridial) portions until the close of Stage e. Early in Stage f they have completely separated from the latter (Plate VIII, fig. 41), and now rapidly become reduced in size, so that by the close of Stage f they have the form of somewhat triangular structures placed in the ventral wall of the heart and pericardium (Plate IX, fig. 43). Inasmuch as the gut has now completely separated from their ventral walls, the generative nuclei have entirely lost their connection with the endoderm—their place of origin. They still lie in the ventral walls of the somites,—a position which they maintain throughout life.

In the next Stage (g) the successive dorsal (generative) portions of the somites of the same side unite with one another, in consequence of the breaking down of the intervening segmental septa, so as to form two tubes (Plate IX, figs. 47, 48), which are the generative glands. The generative glands separate from the floor of the pericardium, except at their front end, where they remain attached to it throughout life. They thus have the form of two tubes closely applied together and placed in the dorsal region of the central compartment of the body cavity.

The Somites of the Twenty-first Pair, or somites of the anal papillæ, never become divided into two parts. The median division remains in connection with the lateral (Plate IX, fig. 44), which, however, as in the case of the other somites, acquires a ventral diverticulum. This hugs the outer side of the nerve-cord, and acquires in late embryos of Stage f an external opening, which, however, is much nearer the middle line than



in the case of the anterior somites, and, indeed, may be described as being common with that of the opposite side. However this may be, the two openings soon become definitely united to form a single opening,—the generative opening, while the tubes themselves persist as the generative ducts. Whether any large portion of the latter are ectodermal in origin, that is to say, derived from a growth of the lips of the opening at its first appearance, it is impossible to say. Kennel asserts that a large part of the generative duct is so derived, but it is obvious that such a statement, as in the case of the anterior segmental organs, cannot be regarded as anything more than an expression of probability. It is impossible to settle the question by sections, and I know of no other method.

From the above description of the origin of the generative organs and their ducts, which is in the essential points identical with that of my tentative preliminary account (No. 50), it is obvious that Kennel has failed to trace the origin of the germinal nuclei. He also differs from me as to the origin of the generative tubes themselves, which, he asserts, come from the dorsal divisions, not of a series of somites, but of one single pair. If his account is correct, which, seeing that he has not observed the origin of the germinal nuclei, I am inclined to doubt, it would appear that the generative tubes of the Cape species differ from those of the West Indian in this respect. He adopts my account of the derivation of the generative ducts and their openings from the lateral divisions of a pair of somites, though, curiously enough, in another place he stigmatises my description as “falsch.”

It thus appears that in *Peripatus capensis* the nephridial portion of the twenty-first somite does not separate from the median or generative portion, but remains in connection with the latter and forms the channel by which the generative part of the cœlom communicates with the exterior. The generative ducts are therefore modified nephridia, but it is important to notice that the connection between them and the generative tubes is not to be compared with the so-called funnel of the



normal nephridia. The latter is merely a special portion of the lateral portion of the somite, and does not seem to be represented in the twenty-first somite. In the female of the West Indian and South American species, as described by Gaffron and Kennel, the case seems to be otherwise. Both these observers have found between the ovary and receptaculum seminis a diverticulum of the oviduct, which ends in a thin-walled vesicle. This structure is called "Ovarian-trichter" by Gaffron, and "receptaculum ovarum" by Kennel; and the latter observer distinctly states that he does not regard it as homologous with the funnel of a nephridium (No. 31, p. 66), apparently because of the thin-walled vesicle (of which he was the discoverer) which closes up its free end. It seems to me, however, that it is this very thin-walled vesicle which renders it almost certain that the structure in question is homologous with the so-called funnels of the normal nephridia, all of which open into thin-walled vesicles of a nature precisely similar to the vesicle of the receptaculum ovarum. Had the latter been absent and the diverticulum of the oviduct opened directly into the body cavity, as Gaffron at first supposed, then there would have been a very strong reason against regarding the diverticulum as homologous with the nephridial funnels. On my view, then, the receptaculum ovarum would correspond to a nephridial vesicle which has been drawn out of the leg portion of the body cavity and placed in the central compartment.

How comes it that this structure is absent from the oviduct of the South African species? In the neotropical species of *Peripatus*, in which the receptaculum ovarum is always present, the generative ducts open between a pair of fully-developed legs. In the South African *Peripatus*, on the other hand, they never open between a pair of fully-developed legs, but always behind the last pair of such; the legs corresponding to the generative nephridia being more or less completely rudimentary (anal papillæ, &c.); and it seems to me not unreasonable to suppose that this abortion of the appendage has carried with it the abortion or non-development of the portion

of the somite which, in the preceding legs, gives rise to the internal vesicle of the nephridia.

It would be of interest in this connection to observe whether the oviduct of the New Zealand species, in which the generative ducts open between a pair of fully-developed legs, possesses a structure corresponding to the receptaculum ovarum.

There are rudiments of two pairs of somites behind the somites of the anal papillæ in Stage E. One of these is just visible in Stage F. They vanish completely at the end of Stage F. No appendages or rudiments of such are developed in connection with them.

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## CHAPTER V.

### GENERAL CONSIDERATIONS ON THE DEVELOPMENT UP TO STAGE F.

There are four points in the development of *Peripatus capensis* which appear to me to deserve a more detailed consideration and comparison, with corresponding processes in other types, than it is convenient to give them in a descriptive account. These are: (1) The incomplete segmentation, and syncytial nature of the embryo; (2) the development of the mesoderm; (3) the development of the vascular system, body cavity and cœlom; and (4) the relation of the blastopore to the mouth and anus.

The last point has already been sufficiently considered and its significance pointed out in my paper "On the Origin of Metameric Segmentation" (No. 51). I see no reason to modify the views there set forth on this subject; on the contrary, recent investigations seem to give them additional support.

(1) I have already, in the second Chapter, dealt to a certain extent with the peculiarities in the segmentation of *Peripatus capensis* both intrinsically and in relation to other forms. I think, however, that the subject is of sufficient importance to deserve a more detailed treatment than it was possible to give it in that place.

There can be but little doubt that the ovum of this species possessed, at a period relatively not very remote from the present, a large amount of food yolk; that it resembled in fact in this respect the ovum of the species now living in New Zealand, and the ova of Arthropoda generally. The large size, combined with the almost complete absence of food-yolk,

can, it appears to me, only be accounted for by supposing that the ovum is passing from the large-yolked to the non-yolked condition, and is intermediate between the ovum of the New Zealand and that of the neotropical species. The ovum<sup>1</sup> of the latter species would on this view have been derived from the large-yolked ovum of some remote ancestor.

There are other instances in the animal kingdom of small ova which there is strong ground for regarding as having been derived from large-yolked ova. The most conspicuous example of this is perhaps that of the Mammalia. Within this class we find both large-yolked and small ova; and the investigation of the former which is now being carried on by Caldwell has particular interest inasmuch as it will show more completely than has been possible hitherto how the development is modified by the loss of yolk. Caldwell's investigations are not yet published, and we do not therefore know whether there is an ovum amongst the lower Mammalia with the property—unique so far as I know—of the ovum of *Peripatus capensis*, viz. the large size combined with the almost complete absence of yolk.

It is this peculiarity which, while it gives the cleavage of the ovum of *P. capensis* a great interest, necessitates great caution in dealing with the general importance of the phenomenon.

I shall assume, then, to start with, that the ovum of the Cape species has only recently lost its yolk, and that it may be compared to an ovum of the New Zealand form from which the yolk has been almost completely dissolved out by some reagent. As a matter of fact, it is impossible, with our present methods, to effect this complete solution of yolk and leave its protoplasmic framework; but what we cannot effect has been done by nature in the most complete manner, leaving an ovum which is little more than a loose protoplasmic sponge-

<sup>1</sup> The ovum of the Trinidad species which has been investigated by Kennel (Nos. 30, 31), and of a South American species which I have had an opportunity of examining, is relatively minute (diameter .04 mm.) and poor in food-yolk.



work, excepting at one point where the protoplasm is more dense. It is at this point only that the cleavage takes place; for the breaking up of the rest of the ovum into irregular masses cannot be regarded as a process<sup>1</sup> in any way related to cleavage, inasmuch as the nucleus takes no part in it.

The cleavage would appear, therefore, to be meroblastic, and, as in meroblastic ova, the protoplasm round the nuclei at the periphery of the blastoderm is perfectly continuous with that of the main mass of the ovum in which the yolk is contained, but from which it is absent in this ovum; that is to say, we have round the periphery of the blastoderm, and lying in the part of it which corresponds to the yolk of large-yolked meroblastic eggs, a number of yolk-nuclei, or rather of nuclei which correspond to the yolk-nuclei of such large-yolked eggs.

But the cleavage is not only meroblastic, it takes place in the same manner as in centrolecithal ova, i. e. the furrows extend only a short distance into the ovum (*vide* Chapter II, pp. 21, 22); the deeper parts of the segments are continuous with each other. Very soon, however, the loosely reticulated protoplasm extends on to the contiguous surfaces of the segments, from which it was at first absent. It thus happens that each segment becomes continuous with all the contiguous segments near the surface, as well as in the deeper parts (*vide* description of segmentation, p. 21, Chapter II). By the continued division of the nuclei at the edge of the blastoderm the embryo acquires an external layer of nuclei, which are absent only at one point—the future blastopore.

Of all the forms of Arthropodan cleavage that I know of, this process seems to resemble most nearly that of the mite *Tetranychus telarius*, as described by Claparède (No. 23). In this form, as in *Peripatus*, the first segmentation nucleus divides at the periphery of the ovum, and not in its centre, as in most centrolecithal ova. There is, however, the greatest possible variety in the position of the first segmentation nucleus in Arthropoda, and the matter does not seem immediately important. The

<sup>1</sup> This process is probably identical with the formation of the non-nucleate yolk-spheres found in many Arthropoda.

same cannot, however, be said about the continuity between the segments. This seems to me a matter of the greatest importance at the present moment. It has long been known that the segments of many centrolecithal eggs are at first connected with one another. In proof of this I need only refer to Balfour's summary of the cleavage of centrolecithal ova in vol. i of the 'Comparative Embryology,' and to any of the recent works on Arthropod development (e. g. Patten, No. 41); that is to say, it has for some time been known that the segmentation of centrolecithal eggs is not a complete cleavage, and, indeed, sometimes does not deserve the name of cleavage at all (e. g. most Insecta). But it has generally been supposed that this continuity is soon lost, and that the final result of segmentation is in all cases a mass of completely separate cells (*vide* Patten, No. 41, pp. 565, 567). According to this view the connections which undoubtedly exist between the majority of cells of the adult is purely secondary (*vide* Fleming, No. 1, p. 74).

Two questions now present themselves: (1) Is this view true in fact? (2) Is it genetically true?

In other words, (1) Is it universally true that there is a stage in the embryonic development of the Metazoa in which all the cells of the body are isolated from one another? (2) Has there been such a stage in the evolution of the Metazoa, i. e. a stage in which the body of the common ancestor consisted of a mass of organically separate cells?

The answer to the first question must be undoubtedly a negative one. The cells arising from the segmentation in *Peripatus capensis* are at no period of development completely isolated units, but retain a connection with one another throughout life. It is true that some of them break away from the rest, and form blood-corpuscles and generative cells, but the greater number present in the adult a connection with their neighbours—a connection which has been derived directly from the connections between the cells of the segmenting ovum. The same fact, as has been shown by Heathcote (No. 27), holds good for *Julus*; and it seems to me highly

probable that the connections between the various adult cells of other Arthropoda with centrolecithal eggs will be found to be derived continuously from the connections between the cells of the segmenting ovum.

But while we must admit that there are cases in which the cleavage is not complete, yet in a great many animals—in all cases of small holoblastic eggs—it seems to be quite certain that the cleavage is complete. It is true that the spheres always touch one another, and there may be an organic connection at the point of contact; but assuming that there is no such connection, the question naturally arises: which of these two processes—the incomplete or the complete cleavage—is, from a phylogenetic point of view, the more correct?

It has generally been supposed that the complete cleavage is the most primitive process, and that the mass of organically distinct and similar cells, such as is found in the morula of a typical development, represents a colonial Protozoon-like ancestor of the whole of the Metazoa. In short, the general view seems to be that the immediate ancestor of the first Metazoon was a multicellular Protozoon, the separate cells of which were all distinct from one another. Can we find any justification in the animal kingdom, as we know it, for this view? Is there any living form constituted in this manner? The answer is, it is hardly necessary to say, a negative one. There is no animal composed of a mass of separate and similar cells. All the colonial Protozoa consist of a number of cells connected with one another by protoplasmic filaments; it may be by long contractile filaments, as in colonial Flagellates and Vorticellæ, or it may be by short laterally springing filaments, as in *Volvox*; and it is by means of these connecting threads that the individuals of the colony effect the little co-ordination of which they are capable.

Further, from an a priori point of view, it seems highly improbable that such a number of disconnected units could have formed a stage in the evolution of the Metazoa. Is it possible, then, that there has not been any such stage, and that the so-called colonial Protozoon stage in the Metazoon onto-



geny is purely secondary, and has been produced by the mechanical requirements of individual development? Answering this question for the moment in the affirmative, we come to the alternative view, viz. that incomplete cleavage is the more primitive process. This view, though it possesses, according to our present knowledge, weaker embryological justification than the first, has a far stronger basis of facts derived from the anatomy of living forms. While amongst the Protozoa there is no counterpart of the fully segmented ovum, there is a comparatively large number of colonial forms in which the individuals are connected by irritable protoplasm, and of multinucleate forms, in which the protoplasm, though more (some ciliated Infusoria) or less (some Rhizopoda) differentiated, is without that definite relation to the various nuclei which is characteristic of the colonial forms and of cells in general.

Metschnikoff (No. 39, p. 132), in discussing this very question, contends that the preponderance of complete cleavage, especially in the lower forms, is a strong argument in favour of the colonial Protozoon origin of the Metazoa. Here I differ with him, for in all colonies that we know of the individuals are connected by protoplasmic filaments, which have arisen, not as the result of fusion, but as the result of the incomplete division of the common parent form. A mass of distinct cells, more or less closely applied to one another, is not a colony in the ordinary acceptation of the term, and it is such a form which, according to what I believe to be the view of Metschnikoff and most morphologists, represents the connecting link between the Protozoa and Metazoa.

But perhaps it will be contended that I am wrong in ascribing this doctrine to them, and that they hold the view that the individuals composing that hypothetical ancestral Metazoon, which is suggested by the cleavage of the ovum, were not completely separate but connected as in living colonies of Protozoa. To this I would reply, that if such be their view, then they can find no justification for it from the development of forms in which complete cleavage occurs. It is rather in such a segmentation as we find in some Sponges



(Marshall, No. 37; Sollas, No. 51), in Alcyonarians (Kowalevsky and Marion, No. 33) and most Arthropoda that we shall have to seek the nearest embryological counterpart of the process by which the Metazoa arose from the Protozoa. If this is so, how are we to account for the frequency of the cases in which the furrows, dividing the ovum, completely separate the segments from each other? In the first place, I would ask, are the cases so numerous as is supposed? It seems to me extremely probable that it will be found, on renewed investigation, that incomplete cleavage takes place in many forms in which it has been assumed that complete cleavage is the rule. The complete cleavage of small ova is such a striking phenomenon, and so readily lends itself to speculative suggestions, and has in this form so dominated the views of morphologists (*vide* especially Flemming's remarks above referred to), that I cannot help feeling that it may, in some cases in which perhaps the observation was difficult, have been assumed to occur on insufficient evidence. And this feeling is rather confirmed by the well-known prevalence of the habit of assuming cell boundaries when they cannot be seen. Almost every embryological memoir bears on its plates numerous examples of this habit.

In the second place, it seems possible that the complete cleavage, found so conspicuously in small ova, may be susceptible of a mechanical explanation. The clean rounded form of the spheres at the moment of division is unlike anything else in the animal kingdom, and is suggestive rather of an intensely active force in the centre of the cell, which compels for the moment the assumption of this form in the protoplasm over which it has dominion, than of a tendency inherited from an adult ancestor. I would refer in this connection to Brook's observations on the total segmentation of *Lucifer* (No. 22). He describes how, at the moment of activity, the segments round themselves off, touching only at one point, while in the intervals of rest they flatten out against one another, and possibly become partly fused. The same phenomenon is found in other Crustacea (*vide* Balfour, No. 17, p. 112), and it

seems fairly generally to happen that at the moments of activity the segments round themselves off, and in the intervals of rest flatten out against each other. These facts seem to me to indicate that it may be possible to find a purely mechanical explanation of complete cleavage. However this may be, it seems pretty clear that the holoblastic segmentation of small ova has not the phylogenetic significance usually ascribed to it.

To sum up, the ancestral Metazoon has generally been assumed to be a colonial Protozoon, and when we examine the evidence for this view we find that the holoblastic segmentation, which really suggested it, is totally opposed to it; and further, that the facts of incomplete cleavage which were thought to be opposed to it are somewhat in its favour, though much more suggestive of another view, which I will now consider.

In Chapter II I suggested that the ancestral Metazoon was not a colonial Protozoon, but a multinucleated Infusorian-like animal with possibly a mouth leading into a central vacuolated mass of protoplasm; and that the evolution of the higher forms has consisted mainly in a definite arrangement of the nuclei and of the specialisation of certain of the vacuoles in the internal protoplasm into the cavities of the organs, and of the protoplasmic strands between into the walls of the latter, and into nerves, muscles, &c.

This is not a new view; it is the old view of the origin of the Metazoa, and has been held recently by Saville Kent (No. 45, vol. ii, p. 480) and others. It is entirely in accordance with the facts of the development of *Peripatus capensis*.

With regard to this development, we have to observe that we cannot speak of cells till a comparatively late period (Stage B), and that the intimate structural change underlying the processes of growth of the young embryo is not an increase of cells, but a multiplication of nuclei. First of all a cortical layer of nuclei, lying in the peripheral layer and entirely surrounding, excepting at one point, the vacuolated spherical mass of protoplasm of which the embryo consists, is differentiated.

The central protoplasm, which contains a few nuclei and a great number of large and small vacuoles to which the nuclei have at first no special relation, protrudes from the point at which the cortical nuclei are absent, as though to extend itself in an amœboid manner in search of food. This is the solid gastrula stage (Plate IV, fig. 20). In it no cell outlines are distinguishable, the whole embryo differing only from, say *Vorticella*, in its large size, and the presence of a definitely arranged layer of nuclei round its periphery.

From this stage the cœlo-gastrula is derived by the simple process of the confluence of the larger central vacuoles to form a single internal cavity, the establishment of the definite opening of this cavity to the exterior, and the arrangement of the central nuclei in the protoplasm lining it (Plate V, figs. 23, 24 *b*). Later the mesoderm appears. It is derived from some of the nuclei already present, which increase in number and arrange themselves in the protoplasm around some of the vacuoles which thus early become specialised into another organ, the cœlom.

Metschnikoff, who has done such important service to biology in drawing attention to the physiological importance of amœboid cells in the organism, has been one of the most prominent advocates of the view that the formation of the gastrula by invagination is a secondary process. He considers that the animal of which the gastrula is the embryonic reproduction—if indeed it ever existed—was preceded by a form in which the endoderm consisted of a vacuolated mass of protoplasm without any definite enteric cavity. So far most embryologists of the present day are with him. But he goes further; he considers that this parenchymatous gastrula or blastula<sup>1</sup>—or as he calls it, *Phagocytella*—was preceded by a hollow blastula-like Protozoon form from which it arose by the migration inwards of certain of the cells of the wall of the blastula. This suggestion as to the origin of the gastrula

<sup>1</sup> I am not quite sure whether he considers that the cortical layer (kynoblast) of his *Phagocytella* was interrupted at any point for the protrusion of the central mass (phagocytoblast).



and the form of the ancestral Protozoon has often been criticised, and it seems to me that the facts suggest, with equal strength, quite another view of the matter, viz. that which I have just hinted at.

There are several ways suggested by embryology in which the passage from the Protozoa to the Metazoa may have been effected; and a most admirable and profound analysis of each of these, and a critical review of our knowledge on this subject, is to be found in chap. xiii, vol. ii, of the 'Comparative Embryology.' I cannot do better than quote the words in which Balfour sums up this review of the facts—"Considering the almost indisputable fact that both the processes above dealt with [delamination and invagination] have in many instances had a purely secondary origin, no valid arguments can be produced to show that either of them reproduces the mode of passage between the Protozoa and the ancestral two-layered Metazoa. These conclusions do not, however, throw any doubt upon the fact that the gastrula, however evolved, was a primitive form of the Metazoa; since this conclusion is founded upon the actual existence of adult gastrula forms independently of their occurrence in development" ('Comp. Emb.,' vol. ii, p. 283; the italics are mine).

These words seem to me to express as clearly now, as they did when they were written five years ago, the state of our knowledge on this subject, and in my opinion neither Metschnikoff's view, nor that which I have just put forward as to the exact method of transition between the Protozoa and Metazoa, can be regarded as anything more than more or less plausible suggestions without any strong basis of fact.

The gastræa theory, in so far as it implies the existence of an ancestral two-layered organism, is still in accordance with known facts, and no discoveries have been made which decisively settle the mode of transition between the Protozoa and Metazoa. As, however, the subject is an interesting one it seems worth while contrasting Metschnikoff's view with that which I have just put forward. But before doing so, I am anxious



to notice one or two points in which Metschnikoff seems to have misunderstood Balfour's views on this subject. Balfour, as is well known, was inclined to the view that the gastræa was preceded by a solid form, such a form as Metschnikoff terms parenchymella, and Metschnikoff himself quotes (No. 39) passages from the 'Comp. Embryology' which show this; and yet Metschnikoff represents Balfour as being opposed to the parenchymella theory. It is not quite clear to me what exactly Metschnikoff means by the parenchymella theory; but if this theory merely postulates the existence of a beast with an outer ectodermal layer and an internal mass of amœboid cells, then I have no hesitation in saying that Metschnikoff is mistaken in regarding Balfour as having been actively opposed to it. It is true that Balfour thought that Metschnikoff's view as to the method of origin of the parenchymella was improbable; but surely one may accept the parenchymella without holding the precise views of Metschnikoff as to its origin, just as one may accept the gastræa theory without pinning one's faith to any particular view of the mode of origin of the gastræa. It appears to me that Metschnikoff, in dealing with both the parenchymella and gastræa theories confuses two questions.

(a) Was there an ancestral gastrula, with the characters attributed to it?

(b) If so, how did this ancestral form itself arise?

If the answer to the latter question falls within the province of the gastræa theory, Balfour did not accept that theory and Metschnikoff is wrong in saying that he was strongly inclined towards it. If, on the other hand, the gastræa theory simply generalises from a large number of anatomical and embryological facts as to the past existence of an animal with a particular structure, and leaves the question of origin out of consideration, then Balfour undoubtedly did accept the gastræa theory, but did not thereby, as Metschnikoff seems to think must necessarily have been the case, reject the Parenchymella. On the other hand, Balfour expressed himself distinctly in favour of the latter, though he did not call it by that title,

for does he not say, and does not Metschnikoff quote him as saying (No. 39, p. 156), that he thought it probable that the ancestors of Cœlenterates possessed a solid endoderm of amœboid cells?

This is not the only point in which Metschnikoff has misunderstood Balfour's views. On p. 141 of No. 39, he ascribes to him the view that an amphiblastula form would represent more nearly than any other the transition between the Protozoa and Metazoa. Balfour maintained no such position, as has been already pointed out by the translator of Metschnikoff's paper on the "Intracellular Digestion of Invertebrates," 'Quarterly Journal of Microscopical Science,' vol. xxiv, p. 107, note.

But to resume: Metschnikoff supposes that the parenchymatous ancestor was preceded by a hollow spherical form, the blastula, the cells of which were all alike; and that the blastula became a parenchymatous gastrula by the migration inwards of cells from its external wall.

I do not understand on what grounds Metschnikoff is so strongly disposed towards the view that the hollow blastula represents a primitive form.

There are many cases, even amongst the Cœlenterates, in which a hollow blastula is not formed and segmentation gives rise to a solid planula; and in the rest of the animal kingdom, the cases, in which segmentation gives rise to a solid embryo are quite as numerous, if not more so, than those in which the reverse holds.

I would even go further than this, and maintain that Metschnikoff's view, that the ectoderm is primitive and the endoderm secondary—arising from the former by inwandering—is not more in accordance with the facts of embryology than the opposite view, viz. that the endoderm is primary, giving rise to the ectoderm by budding-off cells—outwandering as it may be called. In almost all Invertebrate groups there are instances of the latter process, in which the ovum, before or after division into two or more large cells, buds out a number of small cells which form the ectoderm; either itself, or the

large cells produced by it, persisting, and eventually, after the appearance of a central cavity, forming the endoderm.

I do not mean to say that the facts are more in favour of this view than in that of Metschnikoff, but I think they favour the one as much as the other.

But granting the hollow blastula as a possible animal, I agree with Bütschli in thinking that there are great physiological difficulties in the way of accepting the process by which, according to Metschnikoff, it may have become transformed into a solid form. Surely a hollow sphere is in a much more advantageous position with regard to nutrition than a solid one; and yet Metschnikoff supposes that the transformation into the solid form was due to the migration of surface cells into the interior for nutritive purposes. The central part of the animal being empty would require no nutriment, and even if it did, what more convenient arrangement could there be than a layer of cells to pass prepared nutritive substances into it? The ectoderm of *Hydra* or of *Cœlenterates* in general is not fed by the migration of cells from the endoderm, and in short we know of no instance in the animal kingdom of food being carried from one part of an organism to another in actively migrating cells. It seems to me much more likely, if the ancestral Protozoon was a hollow blastula, that the first differentiation would have been into locomotive sentient cells and cells for acquiring food, i. e. the differentiation supposed by the invaginate gastrula hypothesis. For it is clearly necessary that the nutritive cells should be in direct contact with the external medium, and this they are not on Metschnikoff's view.

Then again, what justification do we find in the animal kingdom for the hollow blastula hypothesis? With the possible exception of *Volvox*, I know of no form at all approaching a hollow blastula in structure.

These difficulties are avoided by the hypothesis that the primitive form was solid, which also suits the facts quite as well. (1) It is no longer necessary to suppose the migration inwards of cells. (2) There are a considerable number of



instances in the animal kingdom of lowly organised solid forms, which give a certain amount of justification to the hypothesis of a solid ancestor. There is *Trichoplax* (No. 46), the *Orthonectidæ*, the whole of the Protozoa, the acœlous *Turbellaria*, and finally the Sponges, or at least some of them under certain conditions. The latter case is of particular interest, and deserves a little attention here.

Metschnikoff (No. 38, p. 372) states that *Halisarca*, when overfed with carmine, loses its canals and becomes a mass of amœboid cells containing swallowed food, and surrounded by a common envelope of ectoderm. The same fact has been observed by Lieberkühn in *Spongilla* (No. 36), in winter. From these observations, and others by Hæckel and Carter (quoted by Metschnikoff, No. 38, p. 361), it appears that under certain nutritive conditions, the flagellated endoderm cells of sponges may lose their flagella and become amœboid, and the whole sponge revert to the condition of the larva of *Aplysina* (Schulze, No. 47, Pl. 24, fig. 30) of a protoplasmic network with nuclei at the nodes, and a cortical layer of ectoderm.

Metschnikoff (No. 38) has further observed that in many cases the food of the sponge passes directly into the parenchyma and is not found in the collared endoderm cells; while in other cases it is found both in the cells of the endoderm and parenchyma. These facts, as Metschnikoff points out, seem to imply that the endoderm cells are not mainly nutritive, but that their main function is to cause the currents through the sponge body, and that the food brought by these currents passes into the parenchyma, through the walls of the passages, to be digested by the so-called mesoderm cells.

The collared cells are thus inconstant, and appear to be merely parenchyma cells specially modified under certain conditions and capable of passing back into their original form when the need for them has passed away. When they vanish the canal system also goes and the sponge becomes solid so far as the latter is concerned. Inasmuch as the parenchyma cells, and probably also the cells of the ectoderm, are all connected by their processes (except in the cases in which they break



away and become amœboid), it is clear that the sponge in this condition and in the case of Schulze's larva already referred to, is a syncytium, and but little more than a multinucleated Protozoon. It differs from such a Protozoon simply in the greater development of the vacuoles (spaces between the cells) of the central portions, and in the presence of a distinct cortical layer of nuclei.

In some instances this assumption by a sponge of the Protozoon form is much more marked than in the above cases. I refer to the case of the well-known form *Haliphysema*, described by Hæckel (No. 26) as a sponge with an axial ciliated chamber traversing it, and by Lankester (No. 34) as a multinucleated Rhizopod. It is difficult to believe that either of these distinguished naturalists can have made the mistake implied by their contradictory observations; and the only way of reconciling the latter that I know of, is to be found in the above view, viz. that *Haliphysema*, like *Spongilla* and *Halisarca* possesses under certain conditions, the power of becoming solid: that in certain conditions in which it was found by Hæckel, it approximates to the sponge, while under other conditions in which it has been found by Lankester and Saville-Kent it loses its sponge-like structure and comes to resemble a multinucleated Protozoon. There are certain points in Lankester's description of the soft parts which favour this view, e. g. the obviously reticulated nature of the protoplasm (see particularly fig. 9 in Lankester's paper), the large number of nuclei, and, finally, the germ cells.

These facts, though not in any sense proofs of the view of the origin of the Metazoa for which I am contending, are at any rate suggestive of it, and, so far as they go, in favour of it. That is to say, they suggest the view that there would be two courses open to a Protozoon after it had reached a size too great for the proper nutrition of its central portion, i. e. a size in which the ratio of surface to mass was unfavorable; it would either divide, in which case it would remain a Protozoon, or it would develop from its vacuoles a system of connected and specialised channels with a definite communication to the

exterior at one or more places. In the latter case it would constitute the first stage in the evolution of the Metazoa.

There is no reason to suppose that the protoplasm of such a form, even though partially broken up into areas round the various nuclei, would thereby lose the power of taking in to itself foreign substances which were presented as nutrient; in other words, would not prevent it from discharging the functions discharged by the protoplasm of all Protozoa, and by the parenchyma cells or phagocytoblasts of Metschnikoff.

To sum up, while fully agreeing with Metschnikoff, that the formation of the endoderm by invagination of the wall of a hollow blastosphere is a secondary process, I cannot accept his position that the hollow blastula is a primitive form, or that the formation of the endoderm by migration inwards of the cells is a primary process. It seems extremely probable that the blastula has arisen to provide for the better nutrition of the growing embryo, and that the inwandering and invagination are alike secondary processes, the object of which is, when the proper stage is reached, to get the protoplasm back to its central position and ready for the development of the system of the channels which render its maintenance in the inside possible.

(2) The mesoderm in *Peripatus* arises from certain nuclei in the middle ventral line behind the blastopore. These nuclei may, as I have attempted to show above, fairly be regarded as corresponding with the nuclei in the lips of the blastopore, intermediate in character as well as in position, between the ectodermal and endodermal nuclei. The multiplication of these nuclei gives rise to a primitive streak, which, as in the Vertebrata, is entirely posterior to the blastopore, and is marked by a longitudinal groove—the primitive groove.

This process resembles, in all essential points, the formation of the greater part of the mesoderm in other Tracheata from the walls of the germinal groove, differing only in this, that whereas in the latter the germinal or primitive streak occupies

the greater part of the ventral surface, in *Peripatus* it is confined to the part of the ventral surface behind the anus.

I have elsewhere (No. 49) stated my reasons for agreement with Balfour's view, viz. that such a method of mesoderm formation is probably to be regarded as a modification of archenteric diverticula, such as are found in *Amphioxus*, &c. Whether the origin of mesoderm from the walls of archenteric diverticula is a primitive process or not is open to grave doubt.

It seems to me there is a large body of embryological facts which suggest, at any rate, the view that the mesoderm arose as a result of the differentiation and rearrangement of certain of the nuclei of the amœboid central mass of the ancestral parenchymella or gastrula; that is to say, the facts seem to suggest the following as a possible general view of the origin of the three layers of the Triploblastica.

(a) Starting with a large multinucleated Protozoon, the first advance consists in the differentiation of a cortical layer of nuclei, and of the protoplasm governed by them, into a peripheral layer or ectoderm. This layer was possibly of a plastic nature, and allowed the protrusion of the central mass at one or more points. The central mass would, in consequence of its large size, probably be capable of arranging its vacuoles into a series of thoroughfares through itself from one opening on the surface to another, so that the introduction of nutritive matters to its deeper parts would be possible. On the analogy of the Platyhelminth excretory system we may imagine that the protoplasm of these tracts would acquire the property of throwing out vibratile processes into this system of channels for the purpose of assisting in an effective circulation of the external medium through the body. Such an animal would consist, then, of an ectoderm and a central multinucleate mass which, with Metschnikoff, we may call the meso-endoderm.

(b) The next change would consist in the differentiation of the nuclei of the meso-endodermic mass into two kinds: (a) those governing the protoplasm lining the differentiated vacuoles; and (b) the remainder, which would gradually dif-

ferentiate into various kinds as evolution progressed. The differentiation of the protoplasm around the nuclei would proceed hand in hand with that of the nuclei; the result being a gradually increasing complexity in the tissues of the animal.

The result would be, if the canal system remained complex, —a sponge; if, on the other hand, the canal system simplified and preserved only one opening, the ancestor of the other Metazoa.

It is beyond the scope of this paper to discuss the evolution of the mesoderm. I merely throw this out as a suggestion, which is supported by the manner and order of development of the layers in many animals (a peeling off, so to speak, from the ovum: (1) of ectoderm; (2) of mesoderm; (3) leaving the endoderm as the remaining central mass), and as a completion of the scheme which I have put forward in discussing the manner of passage from the Protozoa to the Metazoa.

Finally, I desire again to draw attention to the fact (1) that the formation of mesoderm in *Peripatus* is essentially a formation of nuclei, which pass to their respective positions and arrange themselves in the protoplasmic reticulum there present; and (2) that the primitive streak is the growing point of the animal, from which almost all the tissues of the body of the adult, viz. ectoderm, endoderm, and mesoderm are formed. This is an important point, to which sufficient attention has not been directed. Almost the whole of the embryo, behind the fifth or sixth somite—not merely the mesoderm, but all the layers—derives its nuclei from the primitive streak. The primitive streak nuclei are therefore not merely mesodermal, but ectodermal and endodermal as well.

3. The last feature in the development of *Peripatus capensis* which it is necessary to notice in its general bearings, is the development of the body cavity and the fate of the coelom.

The coelom, as is well known, is the term applied to a body cavity with certain characters—characters which may be



summed up in the following terms:—(1) The cœlom does not communicate with the vascular system; (2) it communicates with the exterior by nephridial pores; (3) its lining gives rise to the generative products; (4) it develops either as one or more diverticula from the primitive enteron, or as a space or spaces in the unsegmented or segmented mesoblastic bands (in the latter case called mesoblastic somites).

The vascular space has none of these characters, and is known as a pseudocœlic space: it develops either from the blastocœle or from a system of channels hollowed out in the mesodermic tissue of the body. In the Annelida and Vertebrata these two spaces co-exist, and present a well-marked contrast to one another; while in the two other great groups of the animal kingdom—the Mollusca and Arthropoda—the relations of the two systems has not been thoroughly understood. We will first consider the case of the Arthropoda.

The body cavity in the Arthropoda has generally been regarded as cœlomic, in spite of the fact that it presents none of the ordinary cœlomic characters. It communicates with the vascular system, it does not open to the exterior by nephridial pores, its lining does not, so far as is known, develop the generative cells, for the generative glands are continuous with their ducts, and, so far as is known, have no connection with the body cavity. Neither has the body cavity been traced into connection with the undoubted cœlom of the embryo. In all the groups of the Arthropoda mesoblastic somites with a more or less well-marked cavity are formed in the embryo; but the fate of these structures has never been followed. We do not know whether their cavities enlarge and unite with one another and give rise to the body cavity and vascular system of the adult, or whether they shrivel up and disappear, their walls only remaining as part of the mesoderm. From what has been said it is also clear that it is impossible to say whether in the Arthropoda the vascular system is nipped off from the cœlom, or whether it arises as a separate set of spaces in the mesoderm, as in Annelids and Vertebrates.

Now, *Peripatus* is a true Arthropod so far as its body cavity is concerned: thus the heart drives the blood into it, and by means of the paired cardiac ostia sucks the blood out of it; it does not communicate with the exterior by nephridial pores, nor does its lining develop generative cells. We are therefore justified in regarding the body cavity of *Peripatus* as homologous with that of other Arthropoda. It results from this that the study of the development of the body cavity in *Peripatus*, which can be traced with comparative ease, must be of extreme interest, as tending to clear up the question of its coelomic or non-coelomic nature in Arthropoda generally.

Kennel was the first to trace the body cavity of *Peripatus*. He showed that it was in part, at any rate, a pseudocœle, but his work was incomplete in that he failed to follow correctly the fate of the coelom. He thought that the coelom became merged into the body cavity. If this were correct, it would follow that in *Peripatus* the vascular system and coelom would be in communication.

As has been fully shown in the preceding pages, this is not the case. The coelom of *Peripatus* can be traced through the whole development, as a system of spaces shut off at all stages of its growth from the system of body-cavity spaces. In the adult *Peripatus* the coelom is in the following condition: (1) a series of nephridia ending internally in small thin-walled closed vesicles; (2) two dorsal tubes—the generative glands and the ducts of these, which latter are derived from one pair of posterior somites. The pericardium, heart, whole of the body cavity (central, lateral, and leg compartments) are exclusively pseudocœlic in origin.

In *Peripatus*, therefore, the gonads are coelomic, and their ducts what Lankester would call nephrocinic.

The condition of the body cavity and coelom of *Peripatus* will be best appreciated by comparing it with that of the same organs in an Annelid, such as *Lumbricus*. 1. In *Lumbricus* the structures corresponding to the nephridial vesicles of *Peripatus* have swollen up and united with one another in pairs

across the middle dorsal and ventral lines, the separating walls between successive somites for the most part persisting; they constitute the cœlomic body cavity of *Lumbricus*. 2. In *Peripatus* the vascular channels, excepting the heart, are swollen out to wide channels, more or less completely continuous with one another, so as to form four or five main vascular tracts, while in *Lumbricus* they are present minute, branching, well-defined as canals.

On comparing *Peripatus* with other *Arthropoda* in this connection we are at once met with these facts: (1) that in no other *Arthropod*, with the possible exception<sup>1</sup> of certain *Crustacea* and of *Limulus* (Lankester, No. 54), are nephridia, recognisable as such, present; (2) that the cavities of the somites cannot be traced beyond a comparatively early stage of development; (3) that the early stages of the generative organs have not been thoroughly made out.

We may, however, with fair probability predict, from what we know (1) of the development of *Peripatus*, and (2) of the resemblance of its body cavity to that of other *Arthropods*, that when the development of the latter has been fully worked out it will be found—as has been suggested by Lankester (No. 54, p. 517)—that the cœlom of the embryo persists as the generative tubes and their ducts, but for the most part vanishes (possibly giving rise to glands of a doubtful nephridial nature), and that the body cavity and vascular system has an exclusively pseudocœlic origin.

<sup>1</sup> The coxal glands of the young *Limulus*, as described by Gulland (No. 54), and the antennary glands of *Crustacea*, as described by Grobben (No. 55), end internally in a structure, which closely resembles the internal vesicles of the nephridia of *Peripatus*. Lankester, in 1885, commented on the "end-sacs" of the coxal glands of the young *Limulus* as follows (No. 54, p. 516):—"The observations here recorded on the structure and connections of the immature coxal gland of *Limulus* tend to render it probable that the green glands of *Crustacea* are also to be regarded as a pair of modified nephridia;" and he goes on to say that, "it seems not improbable that the so-called 'end-sac' of these glands is not part of the nephridium, but is developed from the connective tissue space (cœlomic space) into which the true tubular nephridium originally opened." With slight modifications this view is entirely borne out by the discovery of the "end-sac" and its mode of development in *Peripatus*.

In the Mollusca the cœlom and vascular space have not been generally sufficiently distinguished from one another. There seems, however, to be no doubt that the pericardial cavity of the Lamellibranchiata and Gasteropoda represents the entire cœlom. The reasons for this conclusion are (1) the pericardial cavity is always shut off from the vascular system; (2) it communicates with the exterior by a pair of nephridia.

The generative organs have no relation to the cœlom, so far as is known, in either of the above Molluscan groups; but in the Cephalopoda the generative cells are developed from the mesoderm lining a certain part of the cœlom. This generative part of the cœlom seems, however, to be shut off in the adult from the viscero-pericardial sac.

This fact, viz. the cœlomic nature of the generative organs of the Cephalopoda, together with the fact that in other Molluscs the generative organs either dehisce into one of the nephridia, which morphologically are part of the cœlom, or possess ducts which open close to or into the nephridial ducts, seems, to say the least of it, in favour of the view that the generative organs of all Molluscs were originally cœlomic and that the present arrangement found in the majority is secondary. The question, of course, can only be settled definitely by embryological investigations, but, unfortunately, embryology does not speak clearly on the point.

There can then, from the point of view of adult anatomy, be but little doubt that the pericardial cavity (and viscero-pericardial and generative sacs in Cephalopoda) alone is cœlomic in the Mollusca, and that the other system of spaces whether simulating a body cavity as in Chiton and other Gasteropoda, or forming a close meshwork of spaces as in Lamellibranchs, are vascular and non-cœlomic spaces; and it is only necessary for embryology to bear out this conclusion to settle the matter definitely. Unfortunately, embryologists have not for the most part sufficiently regarded in their investigations the importance of the point, and, for the majority of Mollusca, we are in ignorance as to the exact method of development



of the pericardium as opposed to the heart and vascular spaces.

Rabl (No. 43), Patten (No. 42 *a*), and Ziegler (No. 53) have described mesoblastic bands in *Planorbis*, *Patella*, and *Cyclas* respectively, arising in the typically Annelidan manner; but Ziegler, so far as I am aware, has alone succeeded in ascertaining what part these bands take in the formation of the pericardium, generative organs and kidney. He has found that the generative cells are derived from the mesoblastic bands; that the pericardial cavity arises as two cavities—one in each band—which subsequently unite; and finally, that the kidneys are hollowed out in certain masses of cells of the bands. These results, if generally applicable, appear to confirm absolutely the anatomical proof of the cœlomic nature of the Molluscan pericardium. It is interesting to notice that in Ziegler's figure (fig. 27) the developing pericardial vesicles have exactly the same relation to the primary body cavity or vascular space, i. e. they lie within it, as the nephridial vesicles of *Peripatus* have to the vascular cavity of the leg.

There are certain animals to which the above general considerations as to the distinctness of the cœlom and vascular system do not apply. I refer more especially to the Nermertinea and Hirudinea. In the Nermertinea, according to Oudemans (No. 40), and in the Hirudinea, according to Bourne (No. 21), structures which it is difficult to believe are not nephridia open into the vascular system. I do not intend to discuss these cases now, because, on the one hand, this paper is already too long, and because, on the other, I do not think our present knowledge is sufficient to enable this to be done with profit. But I venture to submit with regard to them that it is not clear in either case that the vascular system into which the nephridia open is homologous with that of other types. The very fact that there is a communication with the exterior is a strong point in favour of the space being cœlomic; and it should be remembered that comparatively little is known with regard to its development in either group.

In conclusion, I may point out, that whereas in most

animals, e. g. Annelida, Mollusca, the vascular space or pseudocœle appears before the cœlom, in Peripatus the cœlom appears first, and that in Arthropods, at least, the vascular space is in the early stages very commonly occupied by yolk, while the cœlom is entirely free from yolk. This latter fact would seem to imply some connection between the vascular space and the enteric space; and I would also desire to point out that the cœlom, generative glands, and nephridia can, in all animals whose development is at all well known, be traced back to a very early embryonic structure, which appears at the very beginning of development, gives rise to no other structures, and itself arises in very different ways in different animals. The embryonic structure I refer to is in some cases the mesoblastic bands, and in others enteric diverticula. That these two kinds of cœlomic rudiments, as I may call them, are homologous cannot be doubted, but which, if either, of the methods of origin is primitive, cannot in my opinion at present be settled.

SUMMARY OF THE DEVELOPMENT OF, AND OF THE ABOVE  
REMARKS ON, THE CÆLOM AND BODY CAVITY.

It is well known that the vascular system of the Arthropoda is in direct communication with the body cavity, and that the vessels are, for the most part, very rudimentary. In fact the blood is driven by the heart or dorsal vessel into the body cavity, and returned directly through the lateral cardiac ostia into the heart. In no other group of animals does this direct communication exist between the heart and the pericardium.

It is therefore important to determine by the study of development, whether or no the blood-containing body and pericardial cavities of the Arthropoda are homologous with the corresponding structures of other types, in which they do not contain blood.

The development of the Arthropodan heart and body cavity is in most cases extremely difficult to follow on account of the

large amount of food yolk present in the embryos, and there is not, at present, any completely satisfactory history of it.

The development of *Peripatus capensis*, which is a true Arthropod, so far as its body cavity and vascular system are concerned, is comparatively easy to follow.

The coelom appears in the ordinary manner as a series of cavities, one in each mesoblastic somite.

The somites, which are at first ventro-lateral in position, soon acquire a dorsal extension, and the cavity in each of them becomes divided into two parts—a ventral part which passes into the appendage, and a dorsal part which comes into contact but does not unite with its fellow of the opposite side on the dorsal wall of the enteron.

The dorsal portions of the somites early become obliterated in the anterior part of the body, but posteriorly they persist, and those of the same side unite with each other so as to form two tubes which are the generative glands.

The ventral or appendicular portions persist and retain their original isolation throughout life. They give rise to two structures :

(1) To a coiled tube, which acquires an external opening through the ventral body wall at the base of the appendage and constitutes the nephridium of the adult ;

(2) To a small vesicle, which is contained in the appendage and constitutes the internal blind end of the tubular or nephridial portion of the somite. (The opening of the nephridium into the vesicle is funnel shaped, and is commonly known as the internal funnel-shaped opening of the former.)

From the above account it follows (1) that the coelom of the embryo of *Peripatus capensis* gives rise to the nephridia and generative glands, but to no part of the body cavity of the adult ; (2) that the nephridia of the adult do not open into the body cavity.

The body cavity of the adult consists, as is well known, of four divisions :—(a) the central compartment containing the intestine and generative organs, (b) the pericardial cavity,

(c) the lateral compartments containing the nerve-cords and salivary glands, and (d) the portion in the appendage.

Of these, without going into details, it may be said that *a* arises as a space between the ectoderm and the endoderm, *b*, *c*, and *d* as spaces in the thickened somatic walls of the somites. The spaces are in communication with each other.

The heart arises as a part of *a* which becomes separated from the rest. Posteriorly it acquires paired openings into the pericardium. It thus appears that the heart and various divisions of the body cavity of the adult form a series of spaces which have nothing to do with the cœlom. They all communicate with each other and seem to form a series of enormously dilated vascular trunks, of which the heart is the narrowest and alone possesses the property of rhythmically contracting.

To sum up it appears that the cœlom in *Peripatus* is an inconspicuous structure in the adult, and has no connection with the body cavity; while, on the other hand, the spaces of the vascular system are but little subdivided, and form the heart and various divisions of the adult body cavity.

If these results are applicable to the Arthropoda generally, and there is no reason, from the similarity of the adult anatomy, to doubt that they will be found to be so, the following morphological features may be added to those generally stated as appertaining to the group—cœlom inconspicuous, body cavity consisting entirely of vascular spaces.

In Vertebrates and most Annelids, on the other hand, the parts in question are arranged as follows:—Body cavity entirely cœlomic; vascular spaces broken up into a complicated system of channels (arteries, veins, capillaries).

In most Molluscs, finally, the pericardium alone is cœlomic; the vascular spaces being represented by the heart and the more or less complicated system of spaces in the body.



## CHAPTER VI.

### THE CHANGES FROM STAGE G TO BIRTH.

THE changes which take place during and subsequent to Stage G are mainly changes of growth and histological differentiation. The most important organs which have not yet made their appearance by the close of Stage F, are the crural glands and tracheæ. The origin of the latter is, I regret to say, still hidden from me. The remaining organs have acquired, in all essential respects, the adult relations by the close of Stage F.

### THE ECTODERM.

In Stage G, the ectoderm retains the characters already described in Ch. III, p. 54. It forms an extremely thin, much vacuolated layer over the greater part of the body, and the nuclei are far apart and in a single layer (Pl. X, fig. 5). In embryos of this age, the ectoderm does not contract when the embryo is preserved, and no doubt its extreme tenuity is due to this fact. On the ventral organs the ectoderm is thicker and the nuclei in more than one layer and close together. On the dorsal hump also, the ectoderm still remains thick, with a large amount of protoplasm external to the nuclei. The dorsal hump, however, has already begun to atrophy; it eventually completely vanishes.

The general ectoderm possesses a large number of vacuoles, and in certain places the nuclei are aggregated together in masses, and are smaller than elsewhere, forming the rudiments of the future spiniferous sense-organs. The latter give rise to the white spots seen on the skin of embryos of this age.

In *P. Balfouri*, and, to a slight extent, in *P. capensis*,

the dorsal ectoderm contains a number of highly refractile globules (Pl. X, figs. 1—4). These are probably yolk globules. They seem to be most numerous in the dorsal hump. The whole dorsal ectoderm of *P. Balfouri* is thicker than the ventral, and partakes, to a certain extent, of the character of the ectoderm of the dorsal hump.

In the later stages, in embryos just before birth, the dorsal ectoderm is highly protoplasmic and much striated, and contains very few, if any, vacuoles (Pl. XII, fig. 13), while the ventral ectoderm is much vacuolated, and retains the characters it possessed at Stage G. That is to say, the nuclei lie in the outer part of the layer, the inner parts being reduced to fine unstained strands passing between the vacuoles.

The further changes in the general ectoderm need no special description. The nuclei come closer together, the vacuoles disappear, a cuticle is formed on the outer surface, and the adult condition gradually acquired. The claws of the jaws and legs, and the spines of the sense-organs, are special developments of the cuticle.

The following ectodermal organs require a special description, and will be considered separately and apart from the general ectoderm :

1. The ventral organs.
2. The nervous system.
3. The slime-glands and crural glands.

On the origin of the TRACHEÆ I have no observations. They seem to arise very late, and have hitherto escaped my observation.

#### THE VENTRAL ORGANS.

For the origin and general history of these organ I must refer back to Ch. III, p. 59, and to Kennel (No. 30). They consist of segmented thickenings of the ectoderm, placed between the appendages and composed of two halves, which are in contact in the middle ventral line (Pl. X, fig. 5). During Stage G they possess two kinds of nuclei : the surface

layer of oval, and an inner mass of more rounded elements. The latter are much inclined to drop out in the sections, leaving a surface layer of nuclei and thin protoplasmic strands passing inwards.

From what has been said as to their history it is obvious that the ventral organs represent a portion of the ectoderm, from which the central nervous system was constricted off. They correspond in number with the segments, and are therefore twenty in number in *Capensis*.

1. The ventral organ of the first somite is probably, as Kennel has suggested, represented by the cerebral grooves. These become completely cut off from the surface ectoderm and form the hollow appendages attached to the ventral side of the brain of the adult (Pl. X, figs. 2, 3, and No. 20, fig. 19, c, d). The walls of these vesicles appear to consist of nervous tissue.

2. The ventral organs of the jaws (Pl. X, fig. 4, v. o. 1) come to lie in the buccal cavity on each side of the mouth at the base of the jaws. They differ from all the posterior ventral organs in not coming into contact with one another in the middle ventral line. They remain in the ectoderm, and appear to retain a connection with the posterior lobe of the brain, or anterior part of the circumpharyngeal commissure.

3. The ventral organs of the oral papillæ join one another ventrally and become divided into two parts by the lips—an anterior contained in the posterior region of the buccal cavity, into which the salivary glands open; and a posterior part on the ventral side of the body just behind the mouth. The intrabuccal part remains in connection with the lateral nerve-cords (No. 20, fig. 14), and these two connections, together with the interposed ventral organ, contribute what Balfour has called the second commissure between the ventral cords.

The posterior part of this ventral organ behaves exactly as do those about to be described.

4. The two halves, of which each ventral organ of the seventeen ambulatory legs at first consists, join one

another ventrally, remain as part of the ectoderm, and appear to retain a cellular connection with the lateral nerve-cords (Pl. X, fig. 5). I could not be certain of this connection in the case of every ventral organ; but Kennel asserts that it exists, and I am inclined to agree with him.

### NERVOUS SYSTEM.

The early development of the central nervous system is described in Ch. III, pp. 56—58 and 64. In Stage *f* the cerebral grooves are still open (Pl. VIII, fig. 33), and the ventral cords are in close contact and still continuous with the thickened ventral ectoderm. The white matter has also made its appearance along the whole length of the dorsal side of both brain and spinal cord.

In Stage *g* two important changes have taken place. (1) The cerebral grooves have become converted into closed vesicles (Pl. X, figs. 2 and 3) and entirely cut off from the superficial ectoderm. (2) The ventral cords have withdrawn themselves from the ventral ectoderm, though they still appear to be attached to the latter by marked cellular processes (fig. 5, Pl. X).

**The Brain.**—The structure of the brain in Stage *g* is shown by the series of sections figured (figs. 1—4, Pl. X). Excepting the increase in the amount of white matter and the closure of the cerebral grooves it is essentially the same as in Stage *f*. In front the two lobes of the brain, though in close contact, are separate from one another (Pl. X, fig. 1). They are continued forwards into the antennæ as the antennary nerves (vide Ch. III, p. 62). The white matter is dorsal and extends somewhat into the centre of the lobes. It may be described (vide Balfour, No. 20) as consisting of three horns: viz. a dorso-lateral (*a*), a ventro-lateral (*b*), and a dorsal (*e*). It is continued forwards along the dorsal sides of the tentacular nerves.

At a little distance behind the eyes the central lobe of white



matter and the cells dorsal to it become continuous with the same structures on the opposite side (Pl. X, fig. 2). A little farther back the connection between the two brain lobes is effected only by the white matter, the dorso-median patch of cells entirely disappearing (Pl. X, fig. 3). A few sections farther back the latter again appear, and their appearance is soon followed, in the section series, by the separation of the cerebral lobes (Pl. X, fig. 4).

The ventral appendages of the brain have already been dealt with (p. 127).

**The Eyes.**—At the close of Stage *e* the eyes are closed vesicles, connected by their ventral corners with the brain immediately external to the white matter (Pl. VII, fig. 22 *a*). The connection, which is at first a broad one, has in Stage *g* become constricted to a narrow pedicle—the optic nerve—connecting the inner wall of the optic vesicle with the brain (Pl. X, fig. 1); at the same time the nuclei withdraw from the optic nerve, and from the portions of the wall of the optic vesicle and of the brain, which lie next the optic nerve (Pl. X, fig. 1). In this manner the white matter of the so-called optic ganglion of the adult is established, and the optic nerve comes to consist entirely of white matter. The layer which will form the rods in the adult eye appears at a very early stage as a result of the withdrawal of the nuclei of the thick inner wall of the vesicle from the internal surface (Pl. VII, fig. 22 *a*, and Pl. X, fig. 1, *rods*). The pigment and lens have not yet been formed. The eye, therefore, in Stage *g* (Pl. X, fig. 1) consists of a vesicle with a thin outer wall closely subjacent to the epidermis, which is very thin over the eye, and of a thick inner wall lying close to and connected with the brain by a cord of nerve-fibres. The inner wall further presents a patch of white matter at the point of entrance of the optic nerve, and a layer of white matter (the rods) next the lumen of the vesicle. The pigment appears in January at the junction of the layer of rudimentary rods and the nuclei. The lens is formed at about the same time, as a secretion of the wall of the vesicle. It lies within and fills up the cavity of

the vesicle. This condition of the eye is practically that of the adult.

### THE VENTRAL CORDS.

The early history of the ventral cords is given on p. 57. In Stage F they are still in close contact with the ectoderm, but an indistinct line of separation can generally be seen between them (Pl. VIII, fig. 39). In Stage G the separation is complete and distinct, though they still remain connected at intervals by cords of cells with the ventral organs (Pl. X, fig. 5). It is in Stage G also that the **commissures** between the ventral cords, and the main **nerves** first become apparent. The commissures between the two nerve-cords are very numerous. They extend in this stage from the ventro-median corner of the cords towards the ectoderm, where they lie in close connection with some rather loose fibrous tissue, which is found at this stage everywhere beneath the ectoderm. They consist of fibrous matter, and can be easily traced into the white matter of the cords.

The efferent nerves arise from the outer border of the cords, directly from the white matter. They are very numerous (Balfour, No. 20), but there are, opposite each leg, two—the pedal nerves—which are much larger than the others and more easily observed. These two arise, the one immediately in front of the nephridium, and the other behind it. In Stage G, when they are first apparent, they consist of close bundles of fibres passing out from the white matter (Pl. X, fig. 5, *nerve*) and continuous with a loose plexus of fibres placed immediately within the ectoderm of the ventral side of the legs (*neuro-musc.*). It therefore appears that the commissures between the nerve-cords, the efferent nerves, and the fibrous matter beneath the ectoderm, all become distinctly apparent at about the same time in Stage G; but how and when they are developed I am unable to say. As may be seen from an inspection of the sections (Pl. VIII, figs. 37—39) there is in Stage F a certain amount of this fibrous tissue, especially at

the ventro-lateral corners of the body, close to the outer border of the nerve-cord, and in the nerve-cords themselves as the white matter; and I have no doubt that it is present at a still earlier stage, though masked by the large amount of nuclei present. In fact, it may be said of this tissue generally, that it does not become a marked feature of the sections until the organs separate from one another and leave room for the previously closely-packed nuclei to spread out, and, as in the case of the white matter of the nerve-cords, partly to withdraw themselves from it (cf. Pl. X, fig. 5, and Pl. VIII, fig. 39). In whatever manner this tissue may be developed, I think there can be little doubt that it is from its first appearance a continuous tissue, that is to say, the circular fibres at *circ. musc.* in Pl. X, fig. 5, are continuous with the network at *neuro-musc.*, which, in its turn, is continuous with the bundle of fibres forming the nerve, and so with the fibrous matter of the nerve-cords. It thus appears, so far as I have been able to observe the development, that the nerves are not formed as outgrowths from the central nervous system, but are parts of a network which originally existed when the nerve-cords were part of the surface ectoderm. In Stage G, the network is clearly continuous with the surface ectoderm (Pl. X, fig. 5). With regard to the commissures connecting the ventral nerve-cords, it seems to me that they also are differentiated *in situ* from the median ventral ectoderm at a time when the nerve-cords were still parts of the surface ectoderm. I have already said that I do not know the manner in which this network develops; part of it is undoubtedly formed around the ectodermal nuclei, *e.g.* the white matter of the cords, the commissures between the cords; some of it, on the other hand, has, from the first, a relation to the mesodermal nuclei, *e.g.* the circular fibres at *circ. musc.*, and the network on the ventral side of the feet at Pl. X, fig. 5, *neuro-musc.* The nerves, therefore, are to be regarded as special differentiations of a pre-existing network, the origin of which is not known, but which at first pervades and is continuous throughout the whole ectodermal and mesodermal tissues of the body.

## SLIME-GLANDS AND CRURAL GLANDS.

The **slime-glands** are entirely ectodermal products. Their early development has been described on p. 64, and the later changes being simply processes of growth, I have nothing to add to the account there given.

The **crural-glands** appear very late. In embryos of April almost ready to be hatched they have the form of shallow invaginations of ectoderm immediately external to the opening of the nephridium (Pl. XI, fig. 11). They seem to be entirely derived from the ectoderm, but I have no details as to their development. I could find no trace of the enlarged crural gland of the last leg of the male in the oldest embryos which I have examined.

**The Stomodæum and Proctodæum**—The early history of these structures has already been given on pp. 64, 67, 68.

The mesodermal investment of the anterior part of the stomodæum becomes very thick, while that of the posterior part remains comparatively thin. The lining cells secrete a cuticular layer. The anterior part becomes the pharynx, and the posterior the œsophagus of the adult.

The proctodæum also acquires a cuticular lining and a well-marked mesodermal investment. It becomes the rectum of the adult.

## THE ENDODERM.

In Stage G the endoderm is reduced to a layer of extreme tenuity (Pl. X, fig. 5). It soon, however, begins to increase in thickness, and in embryos almost ready for birth has the form represented in Pl. XI, fig. 11. The nuclei are placed in the deeper parts of the layer, and the protoplasm stains deeply and contains a large number of granules. The endodermal part of the alimentary canal is without glandular appendages of any kind. In old embryos the enteron generally contains a deeply-staining material with a number of highly refractile particles in suspension. This substance is probably



a secretion of the endoderm cells. The contents of the alimentary canals of the free-living adults is permeated by a number of similar highly refracting bodies.

#### THE MESODERM.

The later history of the mesoderm, i. e. the tissues derived from the walls of the somites, will best be considered under the following four heads, viz :

1. The muscles.
2. The vascular system.
3. The nephridia.
4. The generative organs.

Whether any part of the cutaneous mesodermal structures are ectodermal in origin is, as I have already hinted in dealing with the nervous system, impossible to decide, because of the intimate connection which is established between the ectoderm and the somatic walls of the somites, at almost the first appearance of the latter (vide pp. 69, 70), and which remains during the whole development (vide p. 131).

#### THE MUSCLES.

The cutaneous muscles arise from the subectodermal fibrous network which has been already mentioned, and which in Stage r was crowded with the nuclei of the ventro-lateral corners of the somites. The fibres of the outer part of this network arrange themselves in a circular manner, and form the circular muscles of the body wall. At first the fibres are extremely scanty (Pl. X, fig. 5, *circ. musc.*), but they soon become more numerous. Nuclei are found at intervals amongst them (Pl. XII, fig. 13). The longitudinal muscles appear somewhat later within the circular muscle in seven patches, viz. two dorsal (Pl. XII, fig. 13), two lateral, two ventro-lateral, and one medio-ventral between the nerve-cords. These patches gradually enlarge into the corresponding muscular bands of the adult. They contain nuclei which have often a peculiar, irre-

gular shape (Pl. XII, fig. 13). The muscles, both longitudinal and circular, are deposited outside the commissures connecting the ventral nerve-cords.

The muscles of the feet seem to be derived from the fibrous plexus shown in Pl. X, fig. 1, and are shown at a later stage in Pl. XI, fig. 11). The origin of the transverse septa dividing the body cavity into a central and two lateral compartments has already been described (pp. 76 and 78, Pl. VI, fig. 9, Pl. VII, figs. 21*a*, 24, Pl. VIII, fig. 39, &c., *v. s.*). They arise as outgrowths of the ventral corners of the somites.

The contractile tissue of the gut wall and internal organs generally, is derived from the wandering cells, which themselves appear to be derived from the walls of the mesodermal somites.

#### THE BODY CAVITY AND VASCULAR SYSTEM.

As was first pointed out by Lankester, the Arthropoda are distinguished from all other animals by the possession of paired ostia, perforating the wall of the heart and putting its cavity in communication with the pericardium. The pericardial cavity of Arthropoda, therefore, contains blood, and in this respect differs fundamentally from the similarly named cavity in other animals. Not only does the pericardial division of the body cavity contain blood, but the general body cavity, and in *Peripatus* all the compartments of the latter are also vascular tracts; and it is important to distinguish by a special name this vascular type of body cavity from the non-vascular or CÆLOMIC type which is found well developed in Annelida and Vertebrata. The term "HÆMOCÆLE," which has been suggested by Lankester for this purpose, seems a convenient one, and I propose to adopt it.

The development of the hæmocœle of *Peripatus* has been already fully described on p. 82, *et seq.*, and p. 93; and I have but little to add to the account there given. It is derived in part from a system of spaces developed within the mesoderm, and in part from spaces arising between the

ectoderm and endoderm. The diagrams (Pl. XIII, figs. 14—17) will enable the reader to understand at a glance the origin of the various parts of the vascular tracts and their relation to the cœlom.

In Stage g the **heart** has the form of a tube with thin walls and flattened nuclei; it lies freely in the pericardial cavity, and cords of cell project from its walls into the latter. These cords, the origin of which I have not been able to make out—they first appear in Stage f (Pl. IX, figs. 43, 45, 46, *c. c.*) when the dorsal divisions of the anterior somites are disappearing—seem to become transformed in the later stages into a very remarkable tissue. The structure of this tissue, which may be called the **pericardial network**, or reticular tissue of the pericardium, will be best seen by reference to Pl. XII, fig. 13, which represents a transverse section through the dorsal part of an embryo shortly before birth.<sup>1</sup> The wall of the heart is prolonged into delicate processes, which are continuous with a network occupying a considerable part of the lateral region of the pericardium. This network contains round nuclei in its nodes, and is continuous with the floor and roof of the pericardium. Sometimes the nuclei occur singly, but often they occur in masses (right hand side of fig. 13), which often have the appearance of multinucleated cells lying freely in the pericardium. A careful examination, however, shows that they are nodes of the network already described, and that they only differ from the other nodes in possessing more than one of the round nuclei. Occasionally an apparently free cell with one nucleus may be seen lying in the spaces of the reticulum. This reticular tissue is, I think, derived mainly from the strings (*c. c.*) of the earlier stages, and it persists as the peculiar cellular tissue which has been described by Gaffron (No. 24) in the pericardial cavity of the adult. Gaffron compares this tissue to the fat bodies of other Tracheates, a comparison with

<sup>1</sup> The apparent fusion of the dorsal and ventral walls of the heart to the dorsal and ventral walls of the pericardium in this figure is due to the contraction of the specimen. The heart at this stage, excepting for the network about to be mentioned, lies quite freely in the pericardium.

which I am inclined to agree, although I am not aware that fat bodies are as a rule present in the pericardium.

Mr. Heathcote, however, informs me that in the Myriapoda a portion of the fat body does lie in the pericardium, and resembles in its relation to the heart the pericardial tissue of *Peripatus*. A tissue exactly like the pericardial tissue is found in the lateral compartment of the body cavity (Pl. XI, fig. 11). It has been noticed by Balfour and Gaffron. It seems to me probable that this tissue, which lies in the vascular system, is of the same nature as the lymphatic tissue of the Vertebrata, with which it undoubtedly presents many points of resemblance. The botryoidal tissue of Leeches (Lankester) and the brown cells of Chætopoda may possibly fall into the same category. The former presents very much the same relations to the vascular system, but the latter differs by lying in the cœlom.

In Stage G the horizontal septum which divided the central compartment of the body cavity into a dorsal (*b. b. c.*) and ventral (*b. b. c.*, Pl. IX, fig. 43) chamber breaks down.

Both the pericardial and lateral compartments of the body cavity (hæmocœle) seem to communicate with spaces amongst the muscles of the body wall. One such set of spaces is especially conspicuous between the ectoderm of the ventral body wall and the circular muscles (Pl. XI, figs. 11). This system of spaces, which is probably segmentally arranged, communicates with the spaces in the legs. It is, I think, the blood in these ventral vascular channels which exudes through the ventral organs when the animals are contracted by the action of chloroform.

The **ostia** of the heart appear to arise in Stage G. I have no satisfactory observations of them. They are, I think, confined to the posterior end of the heart in the Cape species.

The main vascular tracts, therefore, are five in number, or, to put it in another way, the HÆMOCŒLE is divided into five main chambers: (1) the central compartment of the body cavity; (2) the heart; (3) the pericardial cavity; (4) the two lateral compartments or lateral sinuses (in which the nerve-



cord and salivary glands lie). In addition to these there are the leg cavities, which contain the nephridia and communicate with (4). Of these the central compartment, lateral sinuses, and heart are free for the most part from traversing tissue, while the pericardial chamber and the leg cavities are broken up by reticular tissue, and the leg cavities by muscles as well.

### THE NEPHRIDIA.

An account of the nephridia up to Stage F will be found in Ch. IV. By Stage G they have practically attained the adult condition, and to complete my account of their history it will only be necessary to describe their final condition, for which purpose I have chosen a stage shortly before birth. I propose at the same time to give a short recapitulatory account of their whole history, under the head of the somites from which they are respectively derived. The general changes which the somites undergo will be rendered clear by a glance at the diagrams on Pl. XIII, figs. 14—17. It must be remembered that I am only dealing here with the cavity contained in the somites, i. e. the *CÆLOM*, and its immediate lining. The walls of the somites, particularly the somatic walls, become greatly thickened and hollowed out. The tissues and cavities so formed give rise to muscles, connective tissue, and parts of the vascular system, as has already been fully described.

**SOMITES OF THE ANTENNÆ** (p. 86).—The first somites send down a diverticulum outside the brain towards the skin (Pl. VII, fig. 19 *b*, Pl. IX, fig. 50, *s. so.* 1) and then divide into two parts (Pl. IX, fig. 51, *s.* 1). They seem to have completely disappeared by Stage G. The ventral diverticulum of Stage E is obviously the rudiment of a nephridium.

**SOMITES OF THE JAWS** (p. 88).—The second somites do not give rise to even a rudiment of a nephridium. They seem to disappear.

**SOMITES OF THE ORAL PAPILLÆ** (p. 75 et seq.).—The third somites send out a ventral diverticulum (Pl. VII, fig. 21 *c.*),

which acquires an opening to the exterior (Pl. VII, fig. 23 *e.*). They become divided into a dorsal and ventral part (diagram, Pl. XIII, fig. 14), of which the dorsal vanishes, while the ventral persists in connection with the opening above mentioned, and is at first placed in the appendage (Pl. VII, fig. 23 *e.*). This ventral or appendicular part is the nephridium of the somite, and becomes the **salivary gland** of the adult. The general form of this nephridium at the close of Stage F is well shown by the diagram (Pl. XI, fig. 6). It consists of a tubular part (*l. s. t. 3, sal. gl.*), opening in front on the ventral surface of the body (*o. s. 3*) within the lip and ending blindly behind, and of a vesicle (*l. s. v. 3*) opening into the tubular part a little in front of its termination. The structure and relations of these parts to each other are illustrated by the three transverse sections figured on Pl. VIII, figs. 37, 38, and 39, and taken along the lines marked 37, 38, 39 in the diagram (Pl. XI, fig. 6). The subsequent changes which this organ undergoes are unimportant. They are illustrated by the diagram Pl. XI, fig. 7, and by figs. 8 and 9, taken from transverse sections of an embryo shortly before birth, along the lines 8 and 9 in fig. 7.

The tubular part has become much elongated (Pl. XI, fig. 7, *sal. gl.*), so that it now extends a considerable distance behind the point of communication with the internal vesicle. It constitutes the salivary gland of the adult, and lies, as is well known, in the lateral compartment of the body cavity (lateral sinus). The walls of the vesicle (*l. s. v. 3*) have become much thicker. They consist (Pl. XI, fig. 8) of a layer of nucleated, richly vacuolated protoplasm. Finally, the portion connecting the tubular part (*l. s. t. 3*) and the vesicle (*l. s. v. 3*) has become elongated into a tube running forwards from the tube to the vesicle, as shown in the diagram (Pl. XI, fig. 7). This communicating portion, as shown in Pl. XI, fig. 9, is closely applied to the dorsal side of the tubular part.

The internal vesicle, which, together with the communicating tube, has hitherto been overlooked, persists in the adult,

and probably constitutes an important functional part of the salivary gland.

SOMITES OF THE FIRST, SECOND, AND THIRD LEGS (Part III, p. 90 et seq.).—The fourth, fifth, and sixth somites divide early into a dorsal and ventral portion, of which the dorsal vanishes, while the ventral acquires an opening to the exterior and persists as the nephridium. The condition of these nephridia in Stage *r* is shown by Pl. VIII, fig. 40. The subsequent changes are very slight, and may be gathered from an inspection of Pl. XI, fig. 10, which is from a transverse section through the third leg of an embryo almost ready for birth. The nephridium (Pl. XI, fig. 10) consists of a thin-walled internal vesicle contained in the leg compartment of the body cavity and communicating by a straight tube with the external opening on the ventral surface. The wall of the vesicle consists of a ragged protoplasmic layer, with here and there a round nucleus.

SOMITES OF LEGS 4 TO 12.—The early history of the seventh to the fifteenth somites inclusive is similar to that of the somites of the first three legs; but in the later stages the tubular part of the nephridium becomes elongated, coiled, and divided into at least three regions (Pl. XIII, fig. 17, diagram). (1) The part next the external opening is dilated into a vesicle—the external vesicle—which is connected with the external opening by a narrow tube (Pl. XI, fig. 11). (2) The vesicle opens into a long coiled tube, which forms the greater part of the nephridium. It is cut across twice in the transverse section from which fig. 11 was taken. It is continuous with (3) a short terminal portion in which the nuclei are very closely packed together. This terminal portion opens with everted lips into the thin-walled, internal vesicle, and constitutes the so-called funnel of the nephridium. The external opening of the nephridia of the fourth and fifth legs are at first immediately outside the nerve cord, as in the case of the others. Their adult position is due to a secondary shifting.

SOMITES OF LEGS 13 TO 17 (p. 93).—The dorsal divisions of these somites persist as the generative organs, and will

be described below (Pl. XIII, diagrams figs. 15—17). The ventral divisions develop as in the legs immediately preceding.

**SOMITES OF THE ANAL PAPILLÆ** (or in P. Balfouri of the eighteenth legs).—I have nothing to add to the description given on p. 95. They persist entirely as parts of the generative ducts. For descriptions and figures of the isolated nephridia or the seventeen legs of the adult I must refer the reader to Balfour's memoir (No. 20), pp. 32—35, and Pl. XIX, figs. 27, 28. I have nothing to add to his description, excepting the fact that the terminal portions of the nephridia do not open into the body cavity, which is a vascular space and not cœlomic, but, as shown in Pl. XI, fig. 11, and in diagram fig. 17, into a thin-walled vesicle, which is directly derived from the original somite.

I think there can be no doubt that the vesicle of the nephridia of the first three legs is homologous with the internal vesicles of the posterior nephridia and not with the collecting, or external vesicle. A comparison of figs. 10 and 11 on Pl. XI, shows that the tubular part of the first three nephridia is very different from the narrow tube leading outward from the external vesicle in the posterior nephridia; though it is without the closely-packed nuclei in the terminal so-called funnel. Further, the structure of the wall of the vesicle itself resembles that of the internal vesicle of the posterior nephridia and not that of the collecting (external) vesicles.

The external cuticle is only prolonged for a very short distance into the neck of the collecting vesicle.

#### THE GENERATIVE ORGANS.

The early history of these organs has already been fully described on pp. 93—98, and I have but little to add to that description. They first appear in the endoderm as large round nuclei (Pl. VII, figs. 26, 27), which migrate into the splanchnic mesoderm (Pl. VIII, fig. 41) of the dorsal divisions of the sixteenth to the twentieth somites, where they acquire a protoplasmic investment (Pl. IX, figs. 43, 47). The parts of the



somites containing them persist as the generative tubes, and become continuous behind with the twenty-first somite (Pl. IX, figs. 42, 44), which does not divide into a dorsal and ventral part but acquires a ventral opening in the same position as the preceding somites. The opening soon, however, shifts to the middle line, where it joins its fellow, so as to form the single generative opening of the adult. In all probability the greater part, if not all of the ducts of the adult, are derived from the twenty-first somite; the dorsal divisions of the five preceding somites forming the generative glands only.<sup>1</sup>

In Stage g the generative organs form two tubes lying in the central compartment of the body cavity and closely applied to one another in the middle line (Pl. IX, figs. 47, 48).

I cannot say when the generative cells begin to show sexual differences. The appearance of the sections referred to (Pl. IX, figs. 47, 48) would lead one to suppose that the specimen was a female, and I have but little doubt that it was. At the same time, I must mention that I have never seen anything at this stage which I could call a male.

In January sexual differences are undoubtedly manifested by the generative tubes. Those of the females presented very much the appearance of the earlier stage. In the male the nuclei were smaller and more numerous, and the lumen was narrower. In fact, the organs differed very much in the same way that they do in ripe embryos. Pl. XI, fig. 12, is from a transverse section of a female embryo almost ready for birth, and fig. 13 from a male embryo of the same age. At this stage the ovarian tubes communicate with one another at their extreme front ends, and behind where they pass into the ovi-

<sup>1</sup> This view would be confirmed in the case of the female if it could be proved that my suggestion (p. 97) that the receptaculum ovarum of the neotropical species is part of the somite which gives rise to the generative opening and outer part of the generative ducts, and homologous with the internal vesicle of the nephridia. The case of the male is more difficult, but probably the testes (prostates of Moseley and Balfour) only, *i. e.* the parts in front of the swollen vesiculæ seminales (testes of Moseley and Balfour), are alone derived from the dorsal divisions of the generative somites.

ducts. In the male the tubes are considerably twisted ; I could not make out any distinct trace of the vesicula seminalis.

I regret to say that I have not paid much attention to the histological development of the sexual glands. The first trace of the sexual organs is the round nuclei of the endoderm. When and how these acquire a cell body I cannot say. They certainly have the latter by Stage G (Pl. IX, figs. 47, 48). The follicular nuclei are the nuclei of the splanchnic mesoderm, which closely apply themselves to the germinal nuclei as soon as the latter emerge from the endoderm. The follicular nuclei appear, therefore, before the protoplasm of the sexual cells (Pl. VII, fig. 26). In Stage G areas of protoplasm, indistinctly marked off from one another, could be distinguished round the larger nuclei (Pl. IX, figs. 47, 48). In the females of the stage just before birth the boundaries of these areas were slightly more marked, but still indistinct (Pl. XI, fig. 12). In the male of this stage there are no lines separating the protoplasm round the granular nuclei of the testes into areas (Pl. XII, fig. 13).

The general bearing of the facts of development of the coelom and body cavity of *Peripatus* is fully dwelt upon in Ch. V, p. 116. I have but little doubt that the same method of development will be found in other Arthropoda. If I am right in this view it must be admitted that the Arthropoda are coelomate animals, that their generative cells are products of the coelomic epithelium, and that the generative ducts are modified nephridia.

The coelom of *Peripatus* does not extend into a perivisceral or body cavity, but remains small, discharging only the functions of excretion and reproduction. The functions of a perivisceral cavity are discharged by the vascular system, in which indeed the coelom is contained (Pl. XI, figs. 10, 11, 13, and diagram, fig. 17) in exactly the same way as the intestine of a mammal is contained in the coelomic body cavity. The

condition of the cœlom and vascular tracts in the adult and the relation of the cœlom to the vascular body cavity is clearly illustrated by the diagram (Pl. XIII, fig. 17). It is commonly said that in the Arthropoda the generative ducts are continuous with the glands, and in this they are contrasted with the Annelida and Vertebrata. As a matter of fact, however, the generative ducts, in *Peripatus* at least, present exactly the same relation to the generative glands as do the oviducts of a dogfish or earthworm to the ovaries of those animals; that is to say, like the latter, the generative ducts open into the cœlom, and the ova are products of the cœlomic epithelium.

It is important to notice that in *Peripatus* the nephridia are parts of the cœlom (Pl. XIII, diagram, fig. 17), just as they are in Elasmobranchs. They are commonly spoken of in a manner which implies that they have but little to do with the cœlom beyond opening into it. This way of speaking of them is calculated to mislead. The nephridia are direct differentiations of part of the cœlom (vide diagrams, figs. 13—17, and figures illustrating their development).

A negative feature, which has often been put forward as characteristic of the Arthropoda, is the apparent absence of nephridia. The nephridia of *Peripatus* have generally been considered as a primitive and peculiar feature. Lankester,<sup>1</sup> however, some time ago (No. 54, p. 516), suggested that the coxal glands of *Limulus* and the antennary glands of Crustacea were nephridia, and that the peculiar "end-sacs" described by Gulland in the coxal glands of the young *Limulus*, and the internal vesicle of the Crustacean antennary gland described by Grobben (No. 55), were part of a true cœlomic space. The discovery of the end-sacs in *Peripatus*, and of their method of development, seems to confirm Lankester's view. And it is interesting to notice that the end-sac of the Crustacean green gland, as figured by Grobben, resembles somewhat in the structure of its wall the end-sacs of the *Peripatus* nephridia.

\* See above, p. 119.

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## EXPLANATION OF PLATES I AND II.

### *List of Reference Letters.*

*a.* Anterior end. *a.* Anus. *an. p.* Anal papillæ. *At.* Antennæ. *c. g.* Groove in brain. *d.* Dorsal ectodermal thickening. *e.* Eye. *ec.* Ectoderm. *en.* Endoderm. *F. 1 . . . &c.* Feet. *j.* Jaw. *j. s.* Swellings at base of jaws. *L.* Lip. *M.* Mouth. *me.* Mesenteron. *or. p.* Oral papillæ. *o. s.* Opening of salivary gland. *p. s.* Præoral somite. *R.* Rectum. *s. 20.* 20th somite. *s. g.* Salivary glands. *sl. g.* Slime glands. *s. o. 4 and 5.* Nephridia of 4th and 5th legs. *st.* Ectodermal ingrowths into embryonic mouth.

### PLATE I.

All the figures on this Plate, except 15, 17—22, are from fresh specimens.

FIG. 1.—*Per. Balfouri*. Side view of unsegmented ovum, showing polar bodies and dark patch. Greatest length  $\cdot 4$  to  $\cdot 48$  mm.

FIG. 2.—*Per. Balfouri*. Unsegmented ovum with dark patch, but without central clear spot.

FIG. 3.—*Per. Balfouri*. Unsegmented ovum with numerous dark patches, each with a clear centre.

FIG. 4.—*Per. Balfouri*. Ovum with two segments from side.

FIG. 5.—*Per. Balfouri*. Ovum with four segments from animal pole.

FIG. 6.—*Per. Balfouri*. Side view of ovum with four segments.

FIG. 7.—*Per. Balfouri*. Ovum with eight dark segments from animal pole. Greatest length  $\cdot 4$  to  $\cdot 48$  mm.

FIG. 8.—*Per. capensis*. Ovum fully segmented, with mosaic of ectoderm cells and scattered branched endoderm cells. Greatest length (of egg-shell)  $\cdot 56$  to  $\cdot 6$  mm.

FIG. 9.—*Per. Balfouri*. View of ovum from animal pole, as opaque object.

FIG. 10.—*Per. capensis*. Aggregation of the endoderm cells beginning.

FIGS. 11 and 12.—*Per. Balfouri*. Completion of same process.

FIG. 13.—*Per. capensis*. Illustrates the same point. Length of ectoderm patch  $\cdot 32$  to  $\cdot 4$  mm.

FIG. 14.—*Per. capensis*. Another phase of the same process.

FIG. 15.—*Per. capensis*. Side view of ovum from preserved specimen, Cap of ectoderm cells covering half the endodermal mass. Progress of epibole. Diameter  $\cdot 240$  mm.

FIG. 16.—*Per. Balfouri*. Stage in which the endoderm cells are covered by the flatter ectoderm cells. Diameter  $\cdot 32$  mm.

## EXPLANATION OF PLATES I AND II.

FIG. 17.—*Per. capensis*. Side view of embryo. A few endoderm cells exposed.

FIG. 18.—Ventral view of same.

FIG. 19.—*Per. capensis*. Gastrula stage, ventral view. Blastopore distinctly circumscribed. Size .204 mm.  $\times$  .240 mm.

FIG. 20.—Side view of same in outline.

FIG. 21.—*Per. capensis*. Gastrula stage, ventral view. Same stage as Fig. 19, but embryo slightly more elongated.

FIG. 22.—*Per. capensis*. Stage A, showing slightly elongated blastopore with primitive streak at hind end. Greatest length .48 mm. *a*. Denotes the anterior end.

## PLATE II.

All the figures on this Plate are of embryos of *Peripatus capensis*.

FIGS. 23—27.—From the original drawings by Miss Balfour. *a*. Denotes the anterior extremity.

The remainder of the figures on this Plate from drawings by Mr. E. Wilson.

FIG. 23. Stage between A and B. With three somites and elongated blastopore. Length of embryo .7 mm., length of blastopore .45 mm.

FIG. 24. Stage between A and B. With five somites. The blastopore is closing in its middle portion. Length of embryo .74 mm., of blastopore .46 mm.

FIG. 25. Stage B. The blastopore has completely closed in its middle portion and given rise to two openings, the embryonic mouth and anus. The anterior pair of somites have moved to the front end of the body, and the primitive groove is very marked. Length of embryo 1.32 mm.

FIG. 26. Stage C. Embryo, in which the flexure of the hind end of the body has begun; with about thirteen somites. The remains of the original blastopore are present as the mouth, placed between the second pair of mesoblastic somites, and the anus, placed on the concavity of the commencing tail flexure, and still removed from the hind end of the body. Greatest length when lying on its back 1.12 mm.

FIG. 27. Side view of same embryo.

FIGS. 28 and 29.—Stage D (spiral stage).

FIG. 28. A young embryo of this stage, viewed from the side. With commencing antennæ and dorsal projection (*d*).

FIG. 29. Rather older embryo of same stage (end of spiral stage), side view. Eyes (*e*) as pits. Jaws and postoral appendages sprouting. Rudiments of eleven pairs of legs. Length from anterior end of head to bend (*d*) 1.6 mm. *At*. Antennæ. *d*. Dorsal thickening. *e*. Eye. *j*. Jaw. *or. p*. Oral papilla. *p. s*. Præoral somite.

## EXPLANATION OF PLATES I AND II.

### FIGS. 30—34.—Stage E.

Fig. 30. Side view of straightened-out embryo. Antennæ ringed. Buccal fold (*L*) extending round the jaw (*j*) on to the ventral surface. Sixteen pairs of legs. Præoral somite ventrally grooved. Apex of oral papilla perforated. Length from front end of præoral lobe to bend (*d*) 1.76 mm. Eye still as an open pit (it is usually closed at this stage). *d*. Dorsal ectodermal thickening. *e*. Eye. *F*. 1 . . . . *gc*. Feet. *j*. Jaw. *L*. Lip. *or. p.* Oral papilla. *p. s.* Præoral somite.

Fig. 31. Embryo of same stage, in natural position in egg membrane.

Fig. 32. Hind end of embryo of same stage, ventral view. *a*. Anus. *s*. 20. 20th somite. *s*. 19 and 18. Legs of 19th and 18th somites.

Fig. 33. Ventral view of head and segments of jaws and oral papillæ of young embryo of same stage (E). Brain ungrooved. Ectoderm of sides of mouth beginning to grow inwards (*st.*). Oral papillæ perforated. Opening of salivary glands (*o. s.*) at base of oral papillæ. *j*. Jaw. *L*. Lips (buccal fold). *M*. Mouth. *o. s.* Opening of salivary gland. *p. s.* præoral somite. *st.* Ectodermal ingrowth at sides of posterior part of mouth to form stomodæum.

Fig. 34. Same view of slightly older embryo, with sides of mouth quite infolded (*st.*) and a new posterior border to the mouth formed. Brain still ungrooved. References as in Fig. 33.

FIG. 35.—Ventral view of head of embryo intermediate between Stages E and F. Grooves in brain wide and shallow. The lips have grown considerably and have extended behind the openings of the salivary glands, but have not yet joined in the middle line. *At*. Antennæ. *c. g.* Groove in brain. *j*. Jaws. *i. s.* Swelling at base of jaws. *L*. Lips. *M*. Mouth. *or. p.* Oral papillæ. *o. s.* Opening of salivary glands.

FIG. 36.—Stage F. Groove in brain almost closed; the opening is slightly wider anteriorly. Lips complete and folded, salivary opening quite covered by them. Jaws completely enclosed. Swellings at base of jaws closely approximated so as to reduce the mouth opening to a narrow slit. The præoral lobes have completely united with one another (cf. Figs. 33—35). References as in Fig. 35.

### FIGS. 37 and 38.—Stage G.

Fig. 37. Side view of embryo of Stage G. Full number of legs and oral papillæ. Length 5—6 mm. *An. p.* Anal papillæ. *At*. Antennæ. *d*. Dorsal ectodermal thickening. *F*. 1—17. The legs. *me.* Mesenteron. *or. p.* Oral papillæ. *R*. Rectum. *s. g.* Salivary glands. *s. o.* 4 and 5. Segmental organs of 4th and 5th legs. *sl. g.* Slime glands.

Fig. 38. Embryo of Stage G, curled up as in the uterus.









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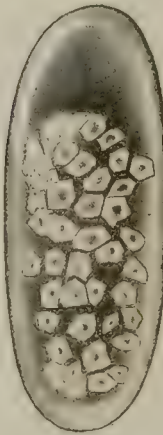
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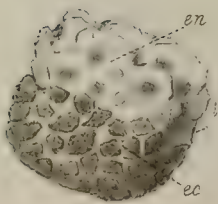
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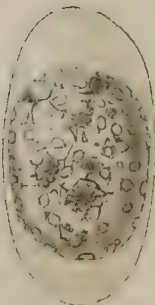
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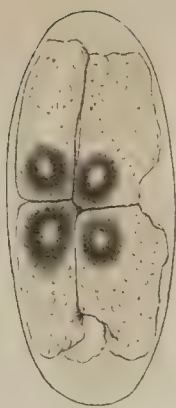
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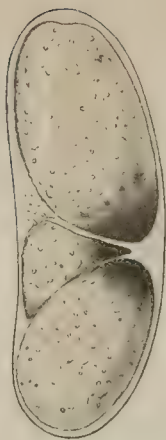
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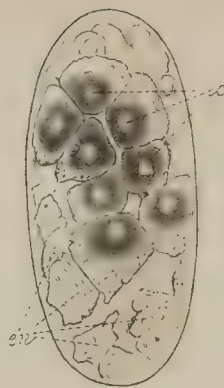
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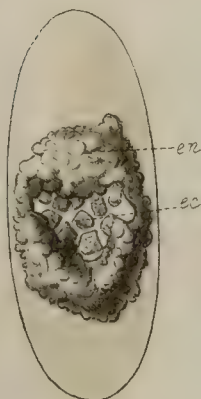
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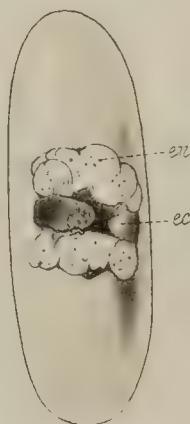
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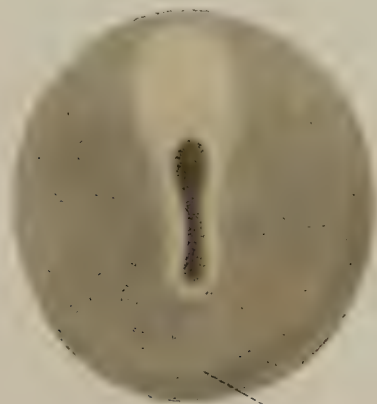
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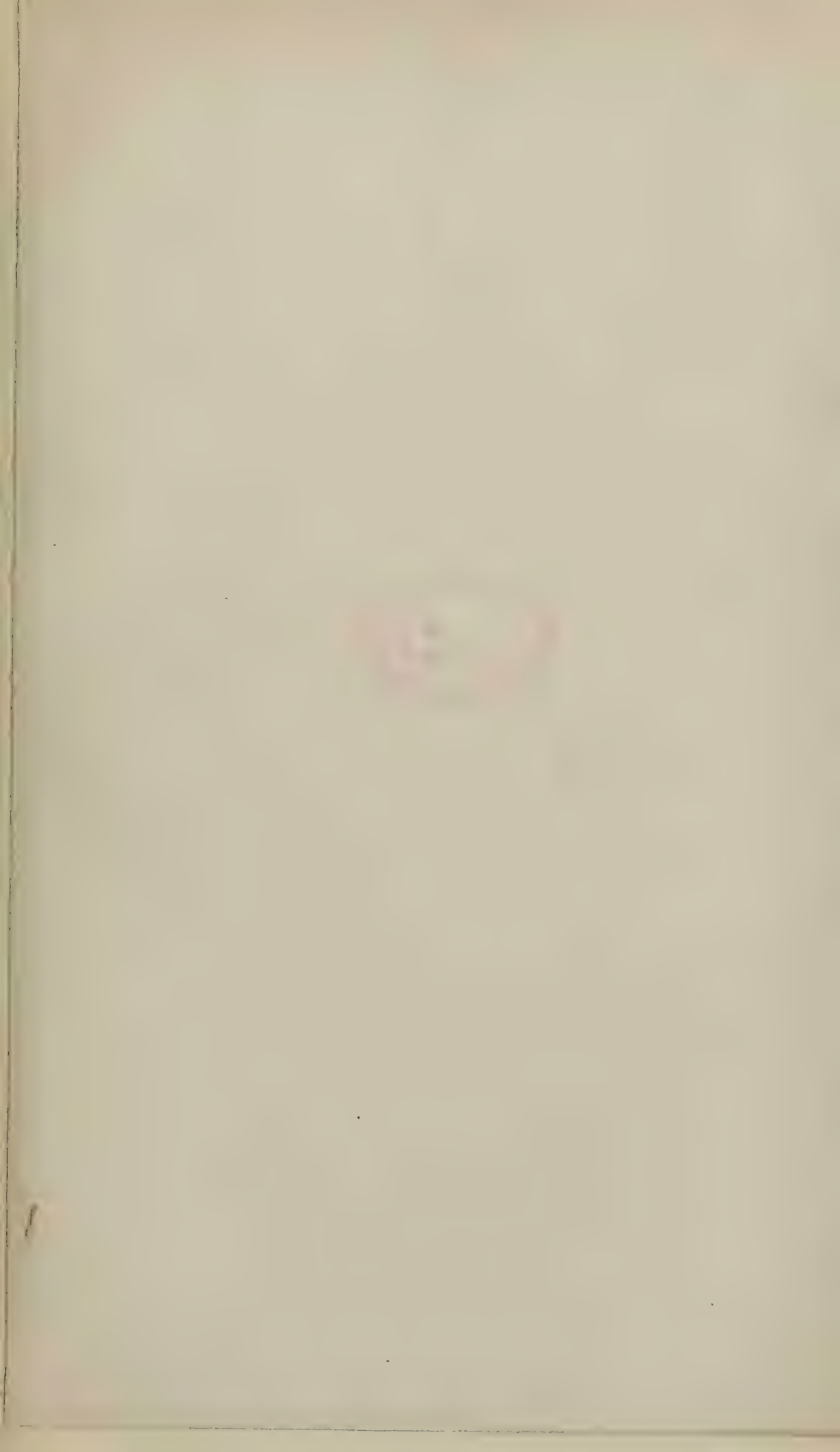
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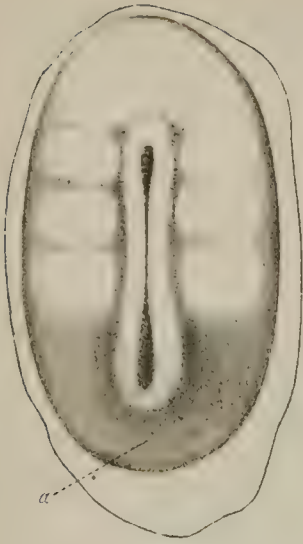


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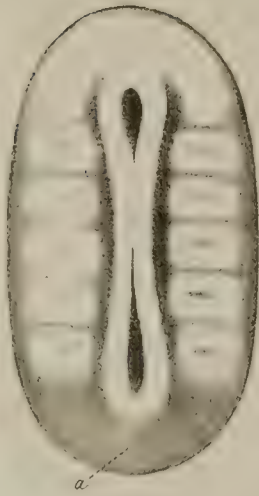




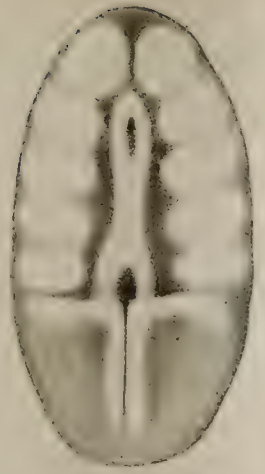




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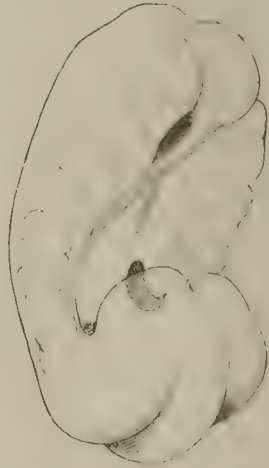
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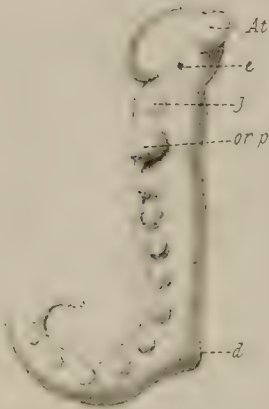
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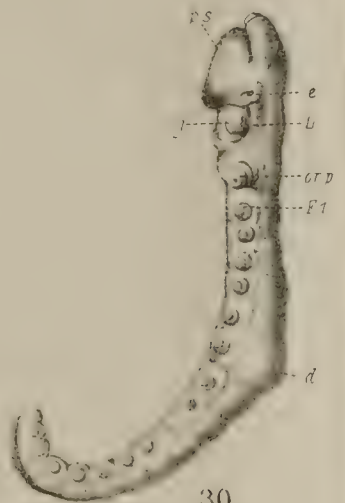
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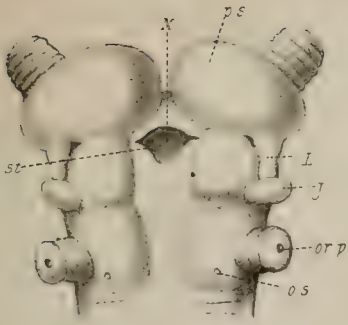
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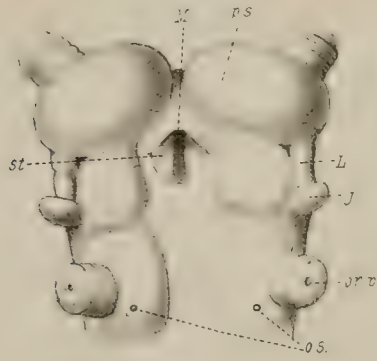
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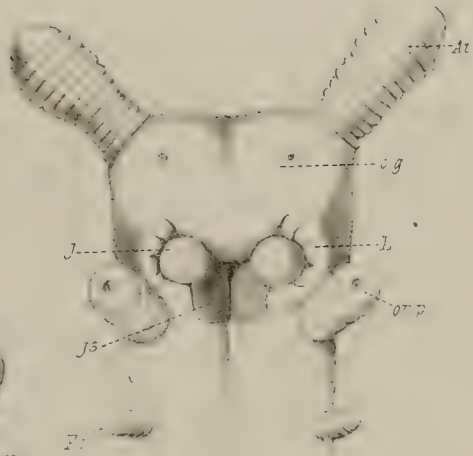
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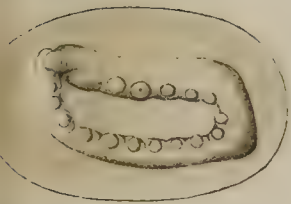
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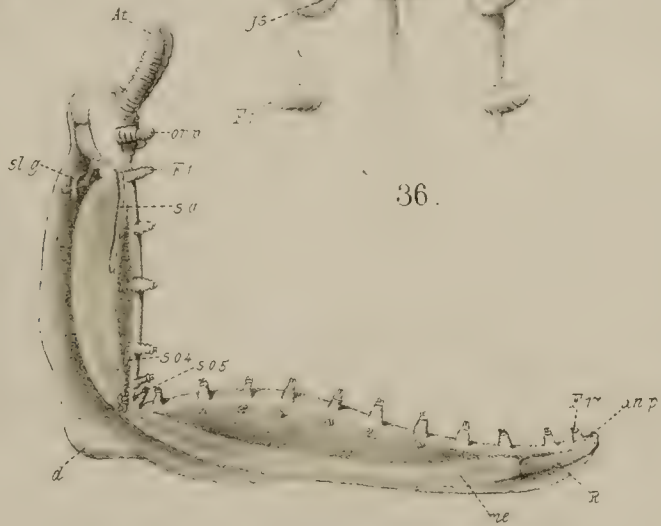
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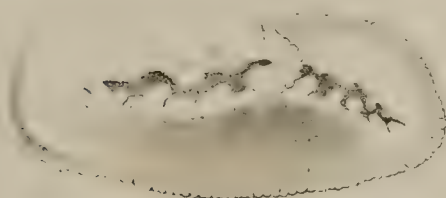
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## EXPLANATION OF PLATES III, IV, & V,

### *List of Reference Letters.*

*p. b.*<sub>1</sub>. First polar body. *p. b.*<sub>2</sub>. Second polar body. *f. n.* Female pronucleus. *m. n.* Male pronucleus. *o. c.* Cavity in centre of ovum. *s. b.* More deeply-staining bodies in extra-nuclear part of ovum. *ec.* Ectoderm. *en.* Endoderm. *e. s.* Egg-shell. *n.* Network. *u. e.* Uterine epithelium. *bl.* Blastopore. *g. g.* Gut of gastrula. *p. a.* Polar area. *p. g.* Primitive groove. *p. st.* Primitive streak. *m. b.* Mesoblastic band.

FIG. 1.—Section through the fertilised ovum of *Peripatus Balfouri* before the conjugation of the male and female pronuclei. The female pronucleus is at the periphery of the ovum. Its reticulum is very loose. Large masses of deeply-staining matter are present. The extra-nuclear reticulum is not denser round either the male or female pronuclei than elsewhere. A large cavity is present in the centre of the ovum. The extra-nuclear reticulum is only drawn in immediately round the two nuclei. Elsewhere it is only indicated by shading. It is completely absent in the centre of the ovum. Peculiar bodies of irregular shape, staining more deeply and continuous by means of processes with the reticulum, are present. They are probably merely expansions of the strands of the reticulum. The male pronucleus is on the opposite side of the ovum to the female, but rather nearer the centre. It does not, however, lie in the same transverse plane as the female nucleus, though very nearly so. It is formed of a network, precisely similar in character to the extra-nuclear reticulum. The membrane round the nucleus is continuous with both the extra- and intra-nuclear reticulum. Deeply-staining bodies are present in the intra-nuclear parts of the network. Near the female pronucleus is the second polar body, with a small portion of the first attached to it. Greatest diameter of female nucleus  $\cdot 029$  mm. The male nucleus measured  $\cdot 025 \times \cdot 016$  mm. Drawn with Zeiss's camera,  $\mathbb{F}$ , oc. 2. Picric acid. *f. n.* Female pronucleus. *m. n.* Male pronucleus. *oc.* Cavity in centre of ovum. *p. b.*<sub>1</sub>. First polar body. *p. b.*<sub>2</sub>. Second polar body. *s. b.* More deeply-staining bodies in extra-nuclear part of ovum.

FIG. 2.—Nucleus of unsegmented ovum of *Peripatus capensis* in spherical stage. Network more diffusely stained than in Fig. 8. Borax carmine. Drawn to same scale as Fig. 8.

FIG. 3.—Nucleus of an ovum with two segments of *Peripatus capensis*. Nucleus divided up into compartments by specially well-marked portions of the nuclear network. The deeply-staining irregularly-shaped masses are almost certainly contained in the strand of the network. The nuclear network is most distinctly continuous with the extra-nuclear reticulum. Reticu-

## EXPLANATION OF PLATES III, IV, AND V.

lum, both of nucleus and cell-substance, slightly stained. Greatest diameter .03 mm. Borax carmine, sublimate and acetic. Zeiss's F, oc. 2, camera.

FIG. 4.—Three nuclei from endoderm of embryo of *Peripatus capensis* of stage of Pt. 1, Pl. II, fig. 19. Zeiss's F, oc. 2, camera.

FIG. 5.—Nucleus of endoderm cell, lying in the gut of an embryo of the same stage. Zeiss's F, oc. 2, camera.

FIG. 6.—Two endoderm masses of *Peripatus capensis*, with their connections and processes. Surface view of sublimate preparation as seen with Zeiss's  $\frac{1}{18}$ th oil imm., oc. 2. Sublimate and acetic.

FIG. 7.—Surface view of a portion of the reticulum connecting the endoderm masses and ectoderm of a fully segmented ovum of *Peripatus capensis*, as seen with a Zeiss's  $\frac{1}{18}$ th oil imm. No endoderm masses shown. Sublimate preparation. Strongly refractile bodies in the strands of the network and sometimes in the meshes.

FIG. 8.—Transverse section through the fertilised ovum of *Peripatus capensis*, showing the nucleus in the spherical stage. The protoplasmic network around the nucleus is denser than elsewhere. A well-marked cavity in the centre of the ovum. Nuclear network for the most part unstained. Nuclear membrane and extra-nuclear reticulum stained. Diameter of nucleus .04 mm. Borax carmine, picric acid.

FIG. 8a.—Nucleus of the last. The lithographer has not been successful in either of these figures, in reproducing the fine intra-nuclear network of the original.

FIG. 9.—Portion of edge of ectoderm of *Peripatus capensis*, with adjacent endoderm masses showing connection between the two. Surface view of sublimate preparation, as seen with Zeiss's C, oc. 2.

FIG. 10.—Ideal diagrammatic transverse section through the fully segmented ovum of *Peripatus capensis*, at about the stage figured in Pl. I, fig. 8, *ec*. Ectoderm. *en*. Endoderm masses, connected by reticulum. *e. s.* Egg-shell.

FIG. 11.—Transverse section through an ovum of *Peripatus capensis* with two segments. The section passes through the centre of the nucleus of one segment. The nucleus has the spindle form, which immediately precedes division. The figure shows clearly the continuity and the similarity between the fibres of the spindle and the fibres of the extra-nuclear reticulum. A well-marked cavity is present in each segment. Greatest diameter of spindle .06 mm. Drawn with Zeiss's F, oc. 2, camera. Sublimate and acetic.

FIG. 12.—Portion of edge of ectoderm of ovum of *Peripatus capensis*, almost at the close of segmentation, as seen with a Zeiss's water imm. 2. Sublimate preparation. The connection between the ectoderm cells is clearly shown, also between the ectoderm cells and the network connecting the endoderm masses. Nucleus of ectoderm indicated. *n*. Network. The apparent granulation of the ectoderm is caused by the fineness of the reticulum.

FIG. 13.—View of endoderm mass of an ovum of *Peripatus Balfouri*,

## EXPLANATION OF PLATES III, IV, AND V.

as seen with a Zeiss's water imm. 2, to show the spongework of which the mass is composed.

FIG. 14.—Transverse section through an ovum of *Peripatus capensis* with eight ectoderm cells, to show the greater density of the network round the nucleus than at the periphery, where it is continued into the reticulum of the next cell. Endodermal masses not indicated. Zeiss's D, oc. 2, camera. Diagrammatic.

FIG. 15.—Transverse section through an ovum of *Peripatus capensis* with about sixteen ectoderm cells, somewhat diagrammatic. The endoderm is indicated. The section shows that the ovum is of the nature of a hollow blastosphere. Zeiss's D, oc. 2, camera.

FIG. 16.—Section through an embryo of *Peripatus capensis* at the stage of Pl. I, fig. 11. The endoderm masses contain a central denser protoplasm, and a number of darkly-staining granules. No nuclei visible in endoderm. Zeiss's D, oc. 2, camera.

FIG. 17.—Transverse section through the uterus, and contained a fully segmented ovum of *Peripatus capensis* (blastosphere stage). Zeiss's c, oc. 2, camera. *ec.* Ectoderm. *en.* Endoderm. *u. e.* Uterine epithelium. *e. s.* Egg-shell.

FIG. 18.—Slightly oblique section through an embryo of *Peripatus capensis* of the stage of Pl. I, fig. 15. Zeiss's c, oc. 2, camera.

FIG. 19.—Portion of ovum of *Peripatus Balfouri* with eight ectoderm cells, showing one of the corner ectoderm cells connected by a reticulum with two endoderm masses. The endoderm masses contain a large number of irregularly-shaped yellowish bodies, *s. b.*; a few of the latter are present in the ectoderm. The outer parts of the ectoderm cells were much vacuolated, and gradually passed into the reticulum connecting them with the endoderm masses. The endoderm was in two main masses, and two or three smaller pieces in the network between ectoderm and endoderm.

FIG. 20.—Transverse section through an embryo of *Peripatus capensis* slightly older than the stage of Pl. I, fig. 15. The endoderm is largely vacuolated, and only a rudiment of the gut-cavity is present. Zeiss's D, oc. 2, camera.

FIG. 21.—Section behind the blastopore of same stage as Fig. 23, showing the most conspicuous part of the polar area. Zeiss's imm. 2, oc. 2, camera.

FIG. 22, *a, b, c.*—Series of sections behind the blastopore of an embryo of *Peripatus capensis*, slightly older than that from which series Fig. 24 were taken. Beginning of formation of primitive streak. Zeiss's D, oc. 2, camera.

*a.* Second or third section behind blastopore. Polar area marked by a slight groove, its nuclei beginning to increase.

*b.* Five sections behind blastopore. Groove absent, but increase of nuclei shown.

*c.* Twelve sections behind blastopore. *p. a.* Polar area.

## EXPLANATION OF PLATES III, IV, AND V.

FIG. 23.—Section through an embryo of *Peripatus capensis* at the gastrula stage (Pl. I, fig. 19). The gut-cavity is still traversed by a mass of much vacuolated endoderm. Zeiss's D, oc. 2, camera. *bl.* Blastopore. *g. g.* Gut-cavity of gastrula. *ec.* Ectoderm. *en.* Endoderm.

FIG. 24, *a—d.*—Series of sections through a gastrula of *Peripatus capensis* of stage Pl. I, fig. 21, before the appearance of the primitive streak. Zeiss's D, oc. 2, camera.

- a.* Five sections in front of blastopore, showing increase of nuclei between ectoderm and endoderm, similar to that which takes place at a later stage behind the blastopore. Endoderm cell lying loose in gut.
- b.* Through middle of blastopore. Blastopore traversed by strands of protoplasm.
- c.* Five sections behind blastopore, showing beginning of polar area in middle ventral line.
- d.* Five sections behind last, through centre of polar area. *bl.* Blastopore. *p. a.* Polar area.

FIG. 25, *a, b.*—Two sections behind blastopore of embryo of *Peripatus capensis*, slightly younger than Stage A (Pl. I, fig. 22). Early primitive streak. No mesoblastic bands. Zeiss's D, oc. 2, camera.

- a.* Immediately behind blastopore. *bl.* Marks position of blastopore in preceding section.
- b.* Nine sections behind the preceding. Large increase of nuclei in polar area, constituting the primitive streak, which is marked by a groove. *p. g.* Primitive groove.

FIG. 26, *a—d.*—Series of transverse sections through an embryo of Stage A (Pl. I, fig. 22). Mesoblastic bands (*m. b.*) have begun to grow forward from front end of primitive streak. Zeiss's D, oc. 2, camera.

- a.* Through the posterior end of blastopore, and two sections behind the front end of the mesoblastic band.
- b.* Hindermost section through the blastopore.
- c.* Through the primitive streak three sections behind the blastopore.
- d.* Through the primitive streak ten sections behind the blastopore. This section shows a portion of the polar area lying unaltered in the deeper part of the primitive streak. *bl.* Blastopore. *p. g.* Primitive groove. *p. st.* Primitive streak. *m. b.* Mesoblastic band.





Fig 1

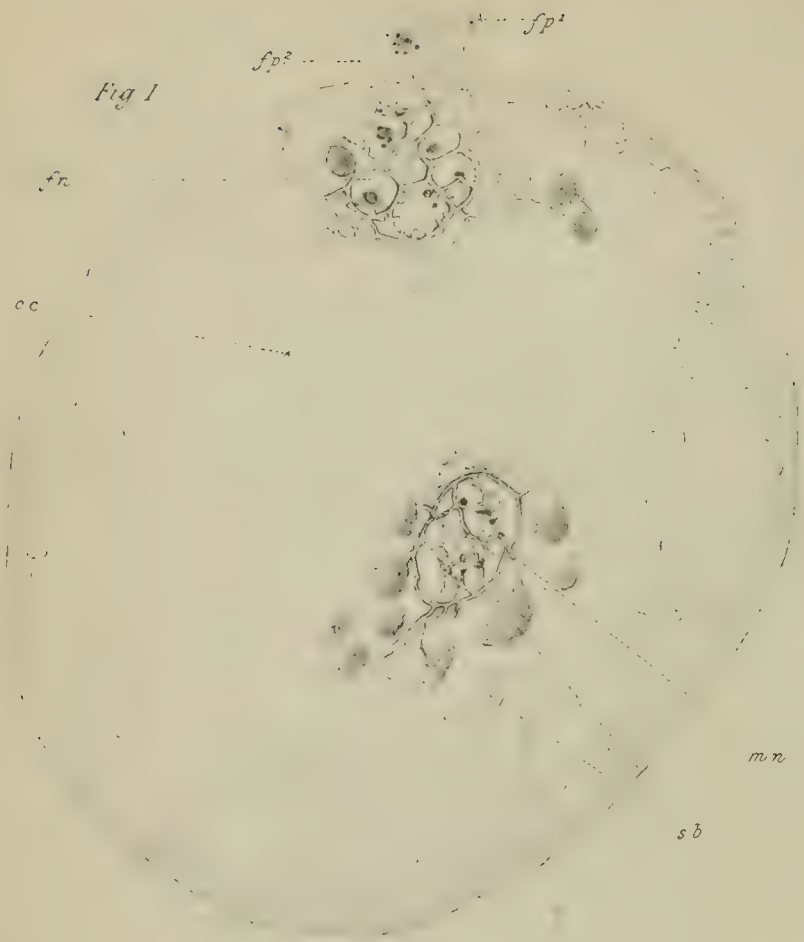


Fig. 2



Fig. 3

Fig. 3.

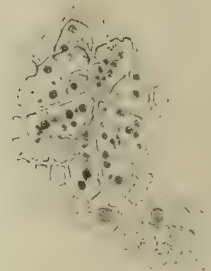


Fig. 9.

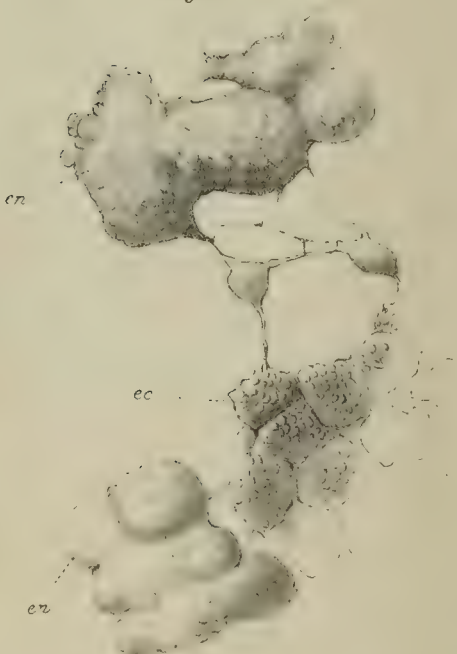


Fig. 10

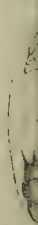


Fig. 8.

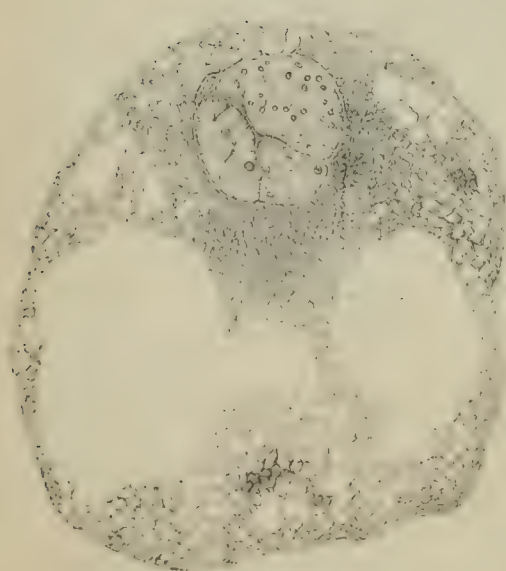


Fig 8a

Fig. 4.



Fig. 7.

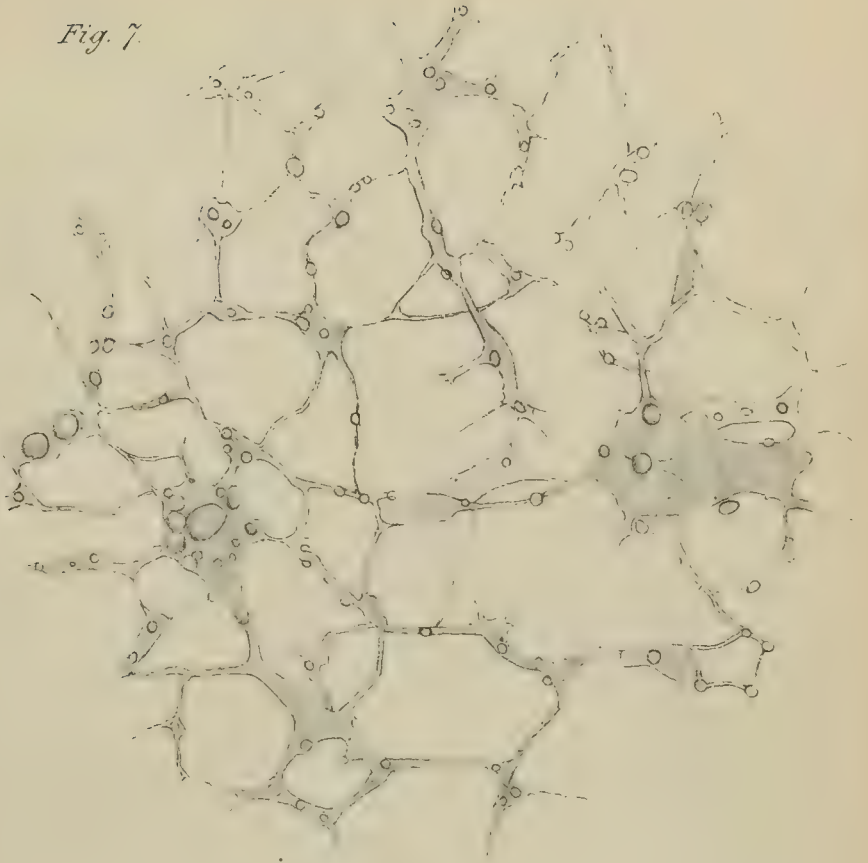


Fig. 6.

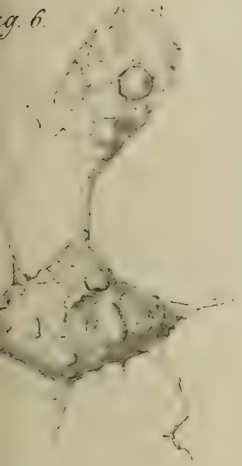


Fig. 11.

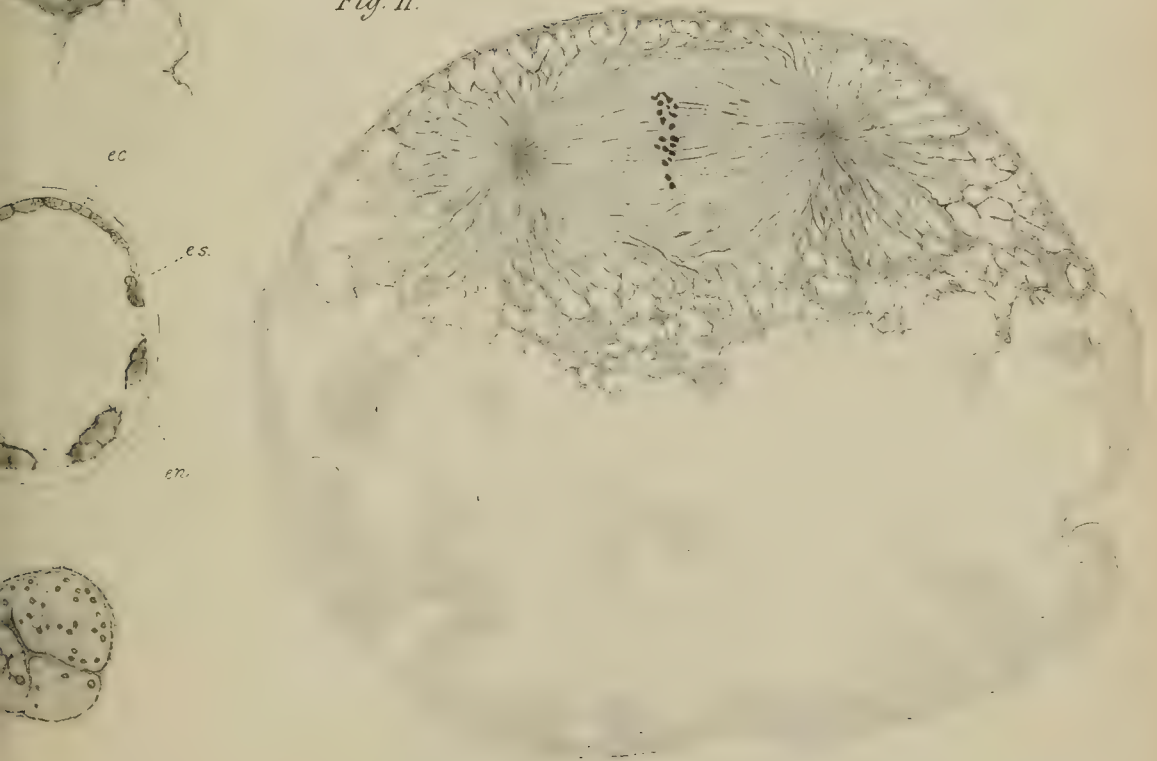








Fig. 12

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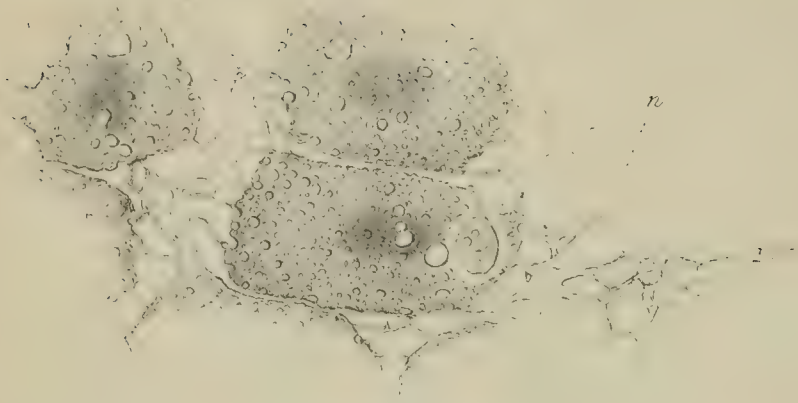


Fig. 13.



Fig. 16.

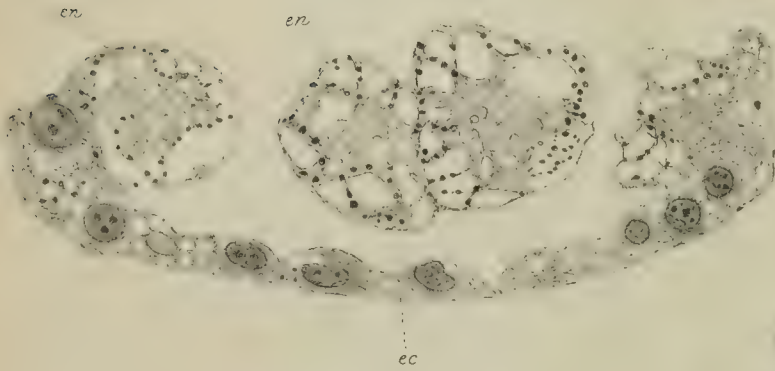


Fig. 20.

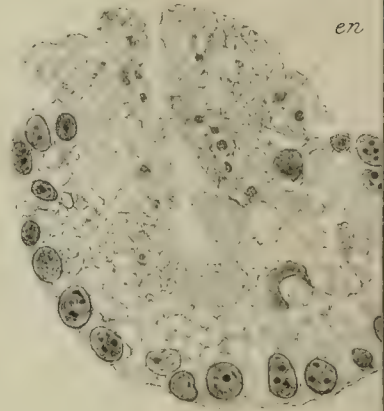


Fig. 19.

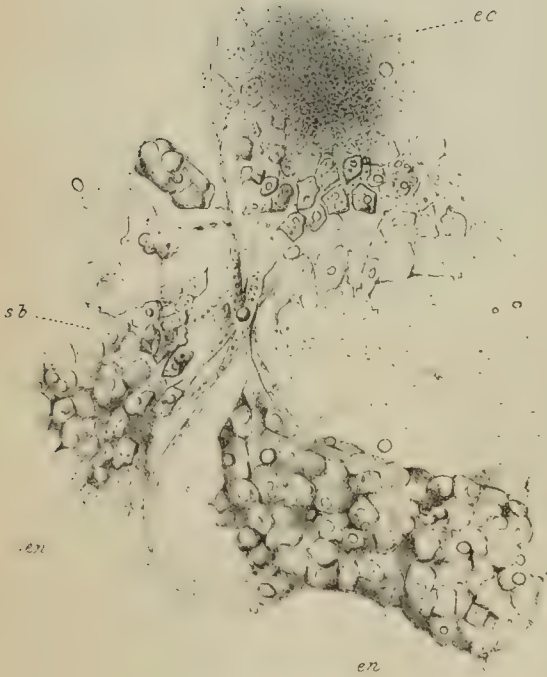


Fig. 21.

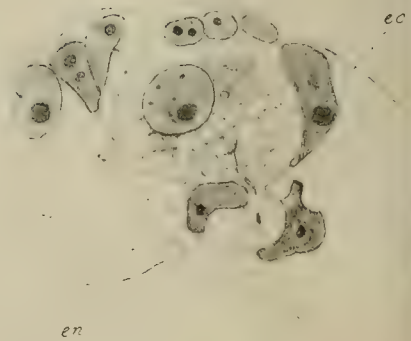


Fig. 14.

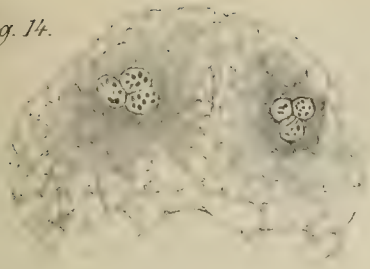


Fig. 15.

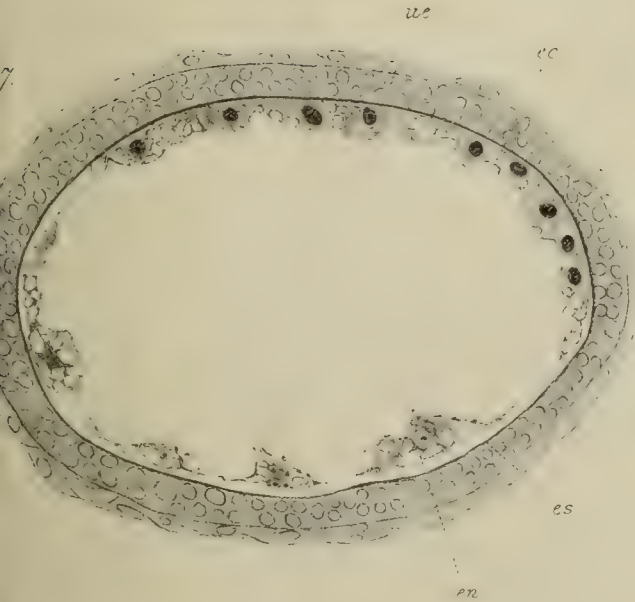
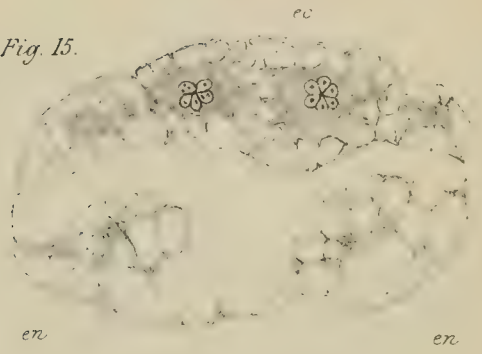


Fig. 18.

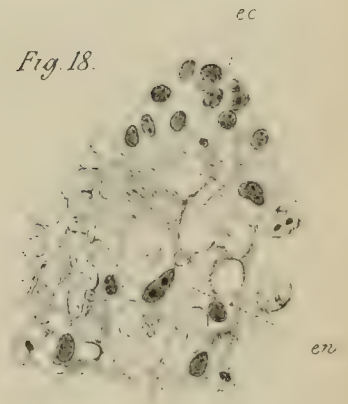


Fig. 22 a

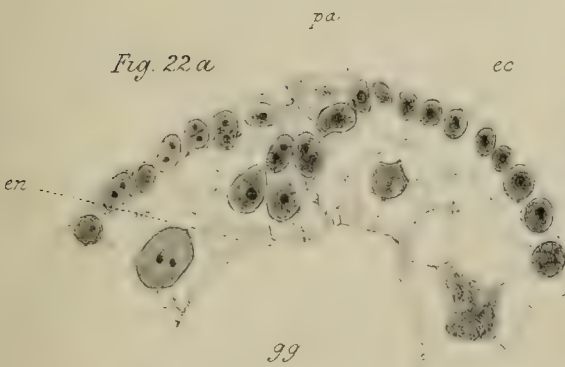


Fig. 22 b

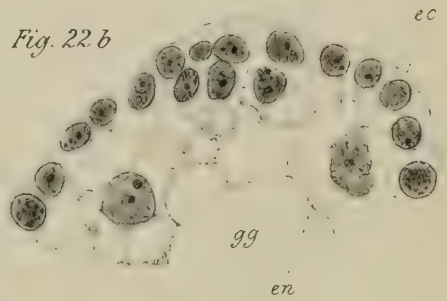


Fig. 22 c.

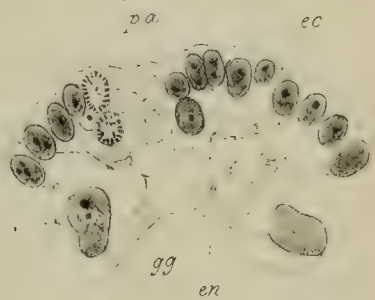








Fig. 24 a.



Fig. 24 b.

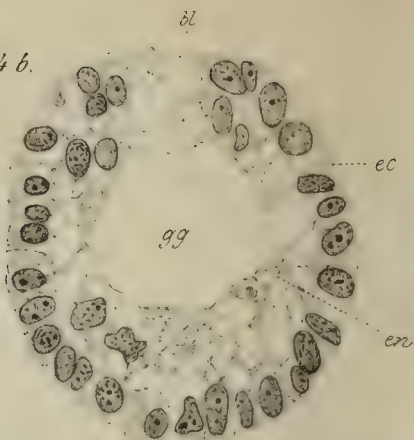


Fig. 25 b.

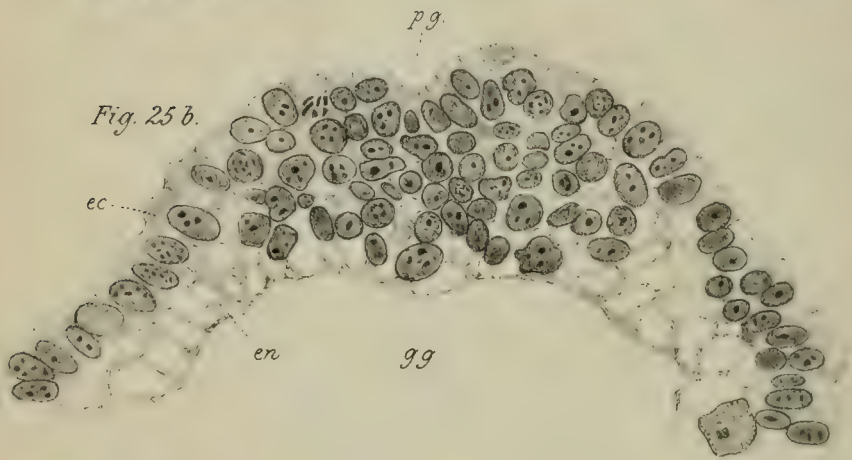


Fig. 23.

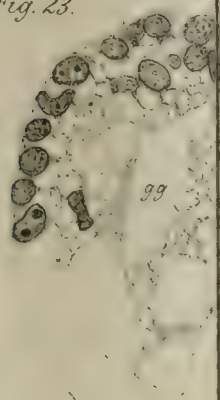
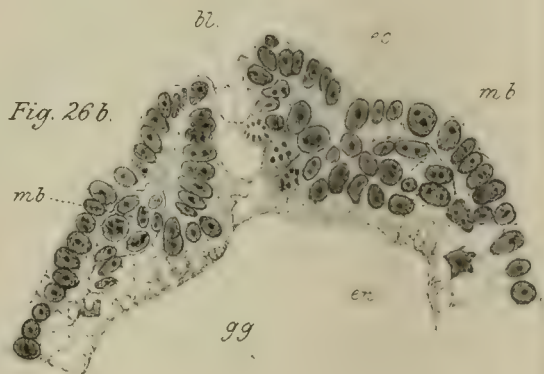
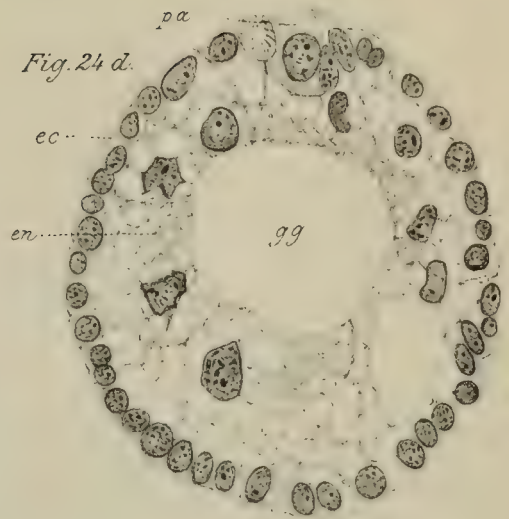
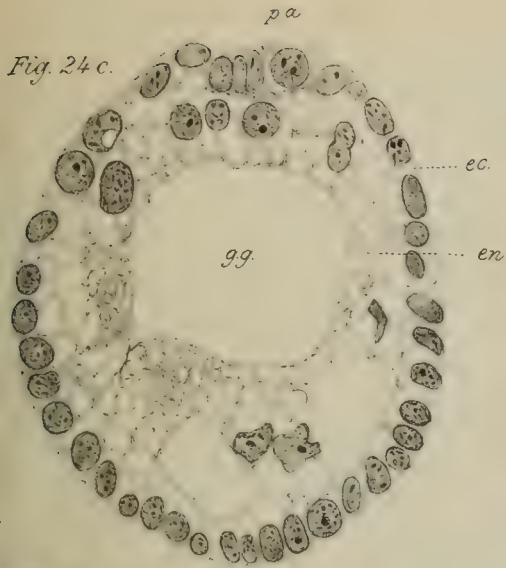


Fig. 26 a.



Fig. 26 b.









## EXPLANATION OF PLATES VI, VII, VIII, & IX.

### *List of Reference Letters.*

*a.* Anus. *am.* Amœboid wandering cells in body cavity (pseudocœle).  
*a. s. ph.* Septum attaching anterior part of pharynx to dorsal body wall, at junction of somites 1 and 2. *a. v.* Anterior diverticulum of nephridium of oral papilla. *b.* Space formed by withdrawal of endoderm from ectoderm. *b<sup>1</sup>.* Space formed in the parietal thickening of the somites. *b. app.* Space formed in appendage. *b. bc.* Space formed by separation of endoderm from ventral ectoderm. *b. bc<sup>1</sup>.* The ventral of the two spaces formed in wall of somites at their ventral corner. *b. h.* Space formed by separation of endoderm from dorsal ectoderm. *b. lat.* Space formed in parietal mesoderm. *b. pc.* The dorsal of the two spaces formed in the wall of the somites at their ventral corner. *br.* Brain. *buc. cav.* Buccal cavity. *c. c.* Cords of cells projecting into pericardial cavity. *c. g.* Cerebral grooves. *c. g.* Groove in brain. *com.* Commissure between the two halves of the brain. *c. o. n.* Circumoral part of central nervous system. *d. n.* Dividing nuclei of endoderm near the lip of the blastopore. *d. s.* Dorsal sheet of somatic mesoderm. *d. s. 1, 2, &c.* Dorsal part of somites 1, 2, &c. *e.* Eye. *ec.* Ectoderm. *en.* Endoderm. *f.* Funnel-shaped opening of tubular part of nephridium into internal vesicle. *f. 1, &c.* Legs. *f. bl.* Line of obliterated blastopore between the mouth and anus. *gen.* Germinal nuclei. *gen. d.* Genital duct. *gen. o.* Generative organ. *g.* and *g. g.* Alimentary canal. *J.* Jaw. *j. s.* Ventral organ of jaw. *L.* Lips. *le.* Internal backward projection of jaw. *l. r.* Limb-ridge. *l. s. 1, 2, &c.* Lateral portions of somite contained in the legs. *l. s. t. 1, 2, &c.* Tubular portion of nephridial cœlom of appendages 1, 2, &c. (segmental organ). *l. s. v. 1, 2, &c.* Internal vesicular portion of nephridial cœlom of appendages 1, 2, &c. *M.* Mouth. *mb.* Mesoblastic band. *me.* Anterior part of thickening of parietal mesoderm of the somites. *m. l.* Muscles of internal projection of jaws. *m. ph.* Muscular wall of pharynx. *m. t.* Posterior part of thickening of parietal mesoderm of the somites. *o. n. 1, 2, &c.* The external opening of nephridium of somites 1, 2, &c. *or. p.* Oral papilla. *o. s. 3.* Opening of somite 3. *p. g.* Primitive groove. *ph.* Pharynx. *ph. m.* Pharyngeal mesoderm from the splanchnic walls of the anterior somites. *p. p.* pre-oral pouch of alimentary canal. *pr.* Proctodæal lining. *p. st.* Primitive streak. *R.* Rectum. *S. 1, 2, 3, &c.* The first, second, and third somites, &c. *sal. gl.* Salivary gland. *sep.* Septum dividing the lateral portion of the somite from the dorsal. *sl. g.* Slime-gland. *S. o. 1.* Rudimentary nephridial portion of somite. *st.* Stomodæum or its lining. *T.* Tongue. *v. en.* Ventra endoderm of alimentary canal derived from the cells intermediate between the

## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

ectoderm and endoderm when the blastopore was open along its whole length. *v. n.* Ventral nerve-cord. *v. o.* Ventral organ. *v. s.* Ventral sheet of somatic mesoderm. *v. sp.* Vascular space. *w.* White matter of central nervous system.

All the figures are of *Peripatus capensis*, and drawn with Zeiss's camera, ob. C, oc. 2, unless it is otherwise stated:

FIG. 1.—Transverse section through a late embryo of Stage A (length .53 mm.), two sections behind the blastopore. The primitive groove is very deep and is hardly to be distinguished from the blastopore. The mesoblastic bands do not extend in front of the hind end of the blastopore. The primitive groove was confined to the front end of the streak. The latter extended through eighteen sections.

FIGS. 2 and 3.—Two transverse sections through an embryo of Stage B (length .65 mm.) with one somite, still solid, and separate from the front end of the mesoblastic band. Primitive streak extended through twenty-one sections.

Fig. 2. Through the single somite which is present. (The section is slightly oblique, passing in front of the somite on the left side.)

Fig. 3. Two sections in front of the anterior end of the somite. The endodermal nuclei at the lips of the blastopore were dividing actively. One such is shown at *d. n.*

FIG. 4.—Section through a late embryo of Stage B (Stage of fig. 25, Pt. I) in front of the mouth. Reduced  $\frac{1}{2}$ .

FIG. 5, *a-f*.—A series of sections through an embryo (length 1 mm.) of the same age as the last (Stage B, fig. 25, Pt. I). Reduced  $\frac{1}{2}$ . Four separate somites could be distinctly made out on each side. Thirty sections were obtained through the streak. The groove extends the whole length of the streak.

*a.* Through the mouth.

*b.* Between the mouth and anus. The blastopore lips have fused; their line of fusion is marked by a slight groove (*f. bl.*).

*c.* Through the hind end of the anus. The mesoblastic bands in this region are not yet broken up into somites.

*d.* Through the front end of the primitive streak, four sections behind the last.

*e.* Through primitive streak, eight sections behind last.

*f.* Through primitive streak, nine sections behind the last.

FIG. 6, *a-d*.—A series of sections through an embryo of Stage C (fig. 26, Pt. I). Reduced  $\frac{1}{2}$ .

*a.* In front of the mouth, through the pre-oral lobes. The anterior wall of the alimentary (*en.*) just touched.

*b.* Through the mouth.

## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

*c.* Between the mouth and anus. Wide separation of the somites. Very thin ventral ectoderm.

*d.* Through the hind end of the body, in the region of the curvature. The embryo is cut in two places, through the anus and through the growing point (primitive streak and groove).

FIGS. 7—12 are from a young embryo of Stage D (fig. 28, Pt. I). The embryos of this age are always much narrower, both dorso-ventrally and laterally, than those older or younger. Reduced  $\frac{1}{2}$ .

Fig. 7. Section through the roots of the budding antennæ.

Fig. 8. Through the anterior part of the mouth.

Fig. 9. Through the posterior part of the third somite, in the region of the outgrowth of the oral papilla (*or. p.*). The sheets of cells extending from the dorsal and ventral ends of the somites are present (*d. s.* and *v. s.*). The endoderm and ectoderm have separated from one another, excepting along the dorsal middle line. The cavity so formed is marked *b. h.* and *b. bc.*

Fig. 10. Through the anterior part of the fourth somite (in front of the region of the future leg), to show the anterior part of the thickening of the somatic mesoderm (*me.*).

Fig. 11. Through the region of the future leg (posterior part of the somite), showing the position of the thickening on the ventral side of the outgrowth.

Fig. 12. Through the fifth somite. The changes which have produced the parietal mass of cells from the somatic mesoderm have not yet occurred here. The somite is partly collapsed dorsally and ventrally.

FIG. 13.—Through the third somite of an embryo of Stage D, slightly older than the last. Reduced  $\frac{1}{2}$ . On the left hand side the section passes through the posterior part of the somite, and shows the developing oral papilla and septum tending to divide the cavity of the somite into a part within the appendage and a part within the body. The first trace of the third system of body cavity (*b. lat.*) is visible.

FIG. 14.—Section through an embryo of Stage D, through the pre-oral somite, brain, and eye. The latter (*e.*) has the form of an open pit. Reduced  $\frac{1}{2}$ .

FIG. 15.—Section through a slightly older embryo, showing a more advanced stage in the brain and eye. Reduced  $\frac{1}{2}$ .

FIG. 16, *a, b.*—Two sections through the mouth of a late embryo of Stage D (fig. 29, Pt. I). Reduced  $\frac{1}{2}$ .

*a.* Through the anterior part in the region of the stomodæal ingrowth.

*b.* Through the posterior part

## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

FIG. 17, *a—d*.—A series of sections through the region of the third somite of an embryo of same age as the last (fig. 29, Pt. I). Reduced  $\frac{1}{2}$ .

- a*. Through the anterior part of the somite, in front of the attachment of the parietal thickening (*me.*). The parietal thickening always appears to be free in front; it is attached behind.
- b*. Point of attachment of parietal thickening to somatic mesoderm.
- c*. Two sections further back.
- d*. Six sections further back through the region of the appendage (*or. p.*).

FIG. 18, *a—c*.—Three sections through the seventh somite of the same embryo as that from which fig. 17 was taken. Reduced  $\frac{1}{2}$ .

- a* and *b* show the leg-ridge, which in fig. 18 *c*—a section through the hinder part of the somite—is enlarged to form the developing fourth leg.

A few sections behind Fig. 18 *c* the cavity of the somite extends into the appendage. The anterior less developed part of the mesodermal thickening lies immediately within the leg-ridge, while the posterior larger part occupies the appendage itself.

FIGS. 19, *a, b*; 20; 21, *a—c* are from sections through young embryos of Stage E. Reduced  $\frac{1}{2}$ .

- a*. Through the head and first somite. The optic pit is closed.
- b*. Through the mouth and first somite. This section shows the developing lip (*L.*). In this and the previous section the mesoderm cells next the stomodæal ectoderm have proliferated to form the commencing pharyngeal and lingual musculature.

Fig. 20. Through the second somite, with the third somite overlapping dorsally.

Fig. 21 *a*. Through the anterior part of the third somite. The limb-ridge (*l. r.*) and the mesodermal thickening with its cavity (*b. lat.*) are well shown.

- b*. Ten sections further back, through the anterior part of the appendage (oral papilla). The mesodermal thickening is much larger.
- c*. Through the centre of the appendage. The somite is nearly divided into two parts by the septum (*sep.*). The portion in the appendage sends down a diverticulum, which lies against the outer border of the nerve-cord and reaches the ectoderm.

FIGS. 22—25 are through a late embryo of Stage E. Reduced  $\frac{1}{2}$ .

- a*. Through the pre-oral region, at the level of the cerebral commissure. The commencing cerebral groove (*c. g.*) is shown.
- b*. Through the mouth and hind end of first somite, showing the rudimentary nephridium (*s. o. 1*). One half of the section only is represented. (Drawn with Zeiss's D, oc. 2).



## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

Fig. 23, *a—e*. A series through the third somite.

*a*. The anterior part of the mesodermal thickening and its cavity (*b'*) is much enlarged. The section passes through the hind end of the jaw (*J.*) and the lip (*L.*).

*b*. A few sections further back. A tube (*a. v.*) ending blindly in front, and opening behind into the limb portion of the somite, is present.

*c*. Nine sections behind fig. 23 *b*, through the point of junction of the portion of the somite in the body (*s. 3*), the portion in the appendage (*l. s. 3*), and the anterior diverticulum (*a. v.* of Fig. 23 *b*).

*d*. Through the centre of the appendage, seven sections behind the last. The anterior end of the fourth somite (*s. 4*) is visible, and rudiment of the slime-gland as an ectodermal ingrowth at the apex the of the oral papilla (*sl. g.*) is present.

*e*. Nine sections behind the last. The external opening of the third somite covered over by the lip (*L.*), which has grown back to this point, and the mesodermal thickening and its cavity (*b. lat.*) of the wall of the fourth somite are present.

Fig. 24. Between the oral papilla and first leg, through the fourth somite, twelve sections behind fig. 23 *e*.

Fig. 25. Through the fourth leg. The eighth somite overlaps dorsally. The leg portion of the seventh somite opens to the exterior (*o. s. 7*). The great ectodermal thickening, which is so conspicuous in embryos of this stage, is cut through at *d*.

FIG. 26.—Transverse section through the anus and twentieth somite of an embryo of Stage D. The rudiment of the proctodæum with its special lining (*pr.*) is present. The germinal nuclei (*gen.*) are present, both in the endoderm and splanchnic mesoderm.

FIG. 27.—Transverse section through an embryo of Stage E, at the region of the seventeenth somite. The germinal nuclei are present in large numbers. The coelom has not yet become divided into body and leg portions (see right hand side of section).

FIG. 28.—Longitudinal vertical section through an embryo of Stage C. The section passes through mouth and anus. The hind end of the body is bent round and projects forward, bearing the primitive streak on its ventral surface. The alimentary canal reaches the anterior end of the body, and the transverse commissure (*com.*) connecting the two halves of the cerebral ganglion is visible in front of the mouth. The modified endoderm (*st.*) or ingrown ectoderm—whichever view of its nature be taken—of the anterior (future dorsal) wall of the stomodæum is present. Zeiss's A, oc. 2.

FIG. 29.—Longitudinal vertical section through an embryo of Stage D. The hind end of the body has grown and become spirally coiled. The primitive streak is still present—but in a rudimentary form—on the ventral surface

## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

behind the anus. It is marked by a slight pit. A section to one side of the middle line of this embryo shows a considerable mass of nuclei in connection with it. The anterior end of the body has been drawn back in such a way that no part of the alimentary canal projects in front of the mouth. The anterior wall of the stomodæum is therefore now inclined dorsalwards and slightly backwards. Zeiss's A, oc. 2.

FIG. 30.—Longitudinal vertical section through the hind end of an embryo of Stage E. The anus is now practically terminal, and the primitive streak aborted. A rudiment of the latter still indeed exists, but there are no lateral masses of nuclei. The rudiment of the proctodæum is present (also in the last figure). Zeiss's A, oc. 2.

FIG. 31.—Longitudinal vertical section through the anterior end of an embryo of Stage E. Zeiss's C, oc. 2. Reduced  $\frac{1}{2}$ . The anterior ectodermic wall of the body has grown forward in the middle line, and separated from the anterior wall of the alimentary canal (cf. fig. 34, Pt. I). The anterior wall of the stomodæum has now become its dorsal wall, and is directed backwards; and an anterior pouch of the alimentary canal lies dorsal to it. The ventral wall of the stomodæum has begun to be formed.

FIG. 32.—Longitudinal horizontal section through the anterior end of an embryo of Stage D. Zeiss's A, oc. 2.

FIGS. 33—42 are transverse sections of an embryo of Stage F.

Fig. 33. Through the first somite, brain and cerebral grooves. The section passes in front of the region where the two halves of the brain are connected, and the eye (*e.*) is just included in the section on the right side. Reduced  $\frac{1}{2}$ .

Fig. 34. The section is taken at the junction of somites 1 and 2, and passes through the posterior part of the brain, the anterior part of the permanent buccal cavity, and the anterior wall of the pharynx (*ph.*) The posterior part of the cerebral grooves (*c. g.*) are seen opening into the buccal cavity, the roof (*T.*) of which becomes the so-called tongue of the adult. The jaw (*J.*) is visible on the right side. Reduced  $\frac{1}{2}$ .

Fig. 35. Through the mouth (*m.*); the opening which leads from the buccal cavity into the pharynx. In consequence of the contraction of the ectoderm, the second somite (*s. 2*) is hardly visible, and the median part of the space *b. h.* is obliterated. Reduced  $\frac{1}{2}$ .

Fig. 36. Behind the mouth, through the oral papillæ (*or. p.*). The slime-gland (*sl. g.*) is cut through just behind its opening, and the anterior part of the ventral cœlom of the third somite (internal vesicular portion, *l. s. 3.*) is shown. Reduced  $\frac{1}{2}$ .

Fig. 37. Immediately behind the junction of the pharynx and mesenteron, through the external opening of the salivary gland (ventral division of somite 3) into the hinder part of the buccal cavity (*buc. cav.*).

# EXPLANATION OF PLATES VI, VII, VIII, AND IX.

Fig. 38. Through the dorsal division of somite 4 and the hind part of the ventral division of somite 3, the opening between the two parts (internal vesicular portion, *l. s. v. 3*, and tubular portion, *l. s. t. 3*) of which are shown. *m. l.* Muscles of internal projection of jaws.

Fig. 38 *a*. One side of a section, a little behind fig. 38, to show the commencing salivary gland (*sal. g.*). Zeiss's D, oc. 2. Reduced  $\frac{1}{2}$ .

Fig. 39. Between the oral papilla and first leg.

Fig. 40. Through the third leg, to show the ventral division of the sixth somite. The tubular portion of this (nephridium of third leg) is a straight tube (the lumen is not distinct, but this was probably due to the contraction of the specimen), opening externally at *o. n. 6*, and internally into the internal vesicular portion (*l. s. v. 6*).

Fig. 41. Through the twentieth somite, in the region of the generative cells. The differentiation of the various divisions of the body cavity has hardly reached this part of the body, *b. h.*, *b. pc.*, *b. bc'*, being only present in a rudimentary form. The endoderm is slightly shrivelled up. The generative nuclei are still in the endoderm, though some of them project into the body cavity. Zeiss's D, oc. 2. Reduced  $\frac{1}{2}$ .

Fig. 42. Through the rectum and anal papillæ (rudimentary eighteenth leg). The dorsal and ventral divisions of the somite are in communication.

FIGS. 43—46 are from old embryos of Stage F. Zeiss's D, oc. 2. Reduced  $\frac{1}{2}$ .

Fig. 43. Through the seventeenth somite, to show the dorsal division of the somite (*d. s.*), which may now be called the generative gland. The gut has separated from the latter, so that the two divisions of the part of the body cavity marked *b. bc'* communicate. The dorsal part of the section only is drawn.

Fig. 44. Through the anal papilla (rudimentary eighteenth leg) and twenty-first somite. The two parts of the somite are in communication, and the ventral has almost acquired an opening to the exterior. This opening will be the generative opening.

FIGS. 45 and 46.—Dorsal parts of two transverse sections from the middle region of the body in front of the generative region; 46 is the anterior. In 45 the dorsal division of the somite (*d. s.*) is not yet obliterated; in 46 it has entirely vanished, and is represented only by the thickened layer of cells which form the ventral wall of the heart.

FIGS. 47 and 48.—Through the generative organs of an embryo of Stage G, in the region where they are detached from the pericardial floor. Zeiss's F, oc. 2.

FIG. 49.—Longitudinal vertical section through the anterior part of the body of an embryo of Stage F. Reduced  $\frac{1}{2}$ .

FIG. 50.—One side of a transverse section through a young embryo of Stage

## EXPLANATION OF PLATES VI, VII, VIII, AND IX.

**r.** To show the latest stage of the rudimentary nephridium of the first somite (*s. o. 1*), in close contact with the outer side of the hind part of the brain (a few nuclei of the latter are indicated). Zeiss's D, oc. 2. Reduced  $\frac{1}{2}$ .

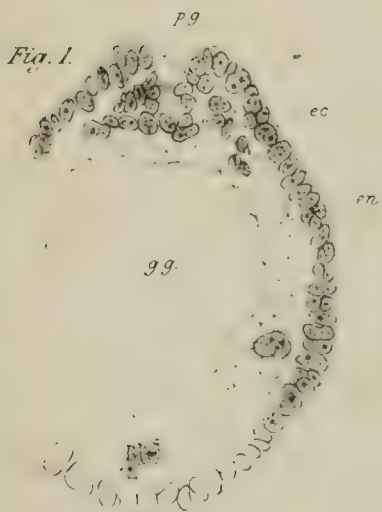
**FIG. 51.**—One side of a transverse section through the brain of a late embryo of Stage **r**. To show the two separate parts of the first somite. The cerebral grooves are closed. Reduced  $\frac{1}{2}$ .

**FIG. 52.**—Transverse section of the sixth leg of an old embryo of Stage **r**. To show the funnel-shaped opening (*f.*) of the tubular portion of the nephridium into the vesicular internal portion (*l. s. v.*), and the relation of the latter to the body cavity (pseudocœle) of the leg (*b. app.*). Zeiss's D, oc. 2. Reduced  $\frac{1}{2}$ .

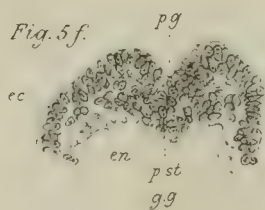
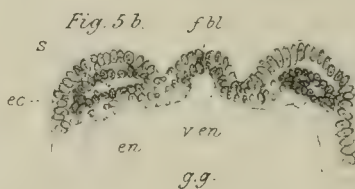
**FIG. 53, a and b.** Longitudinal horizontal sections of two contiguous legs of an embryo of same stage as last. Reduced  $\frac{1}{2}$ .



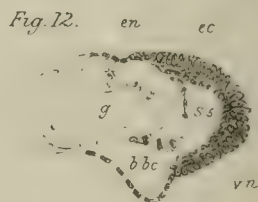




*Fig. 3.*

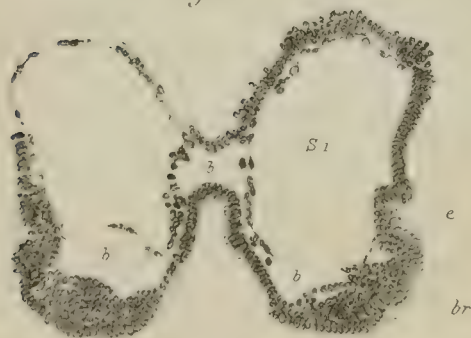


*Fig. 7.*



*Fig. 9.*

*Fig. 14.*



*Fig. 13.*



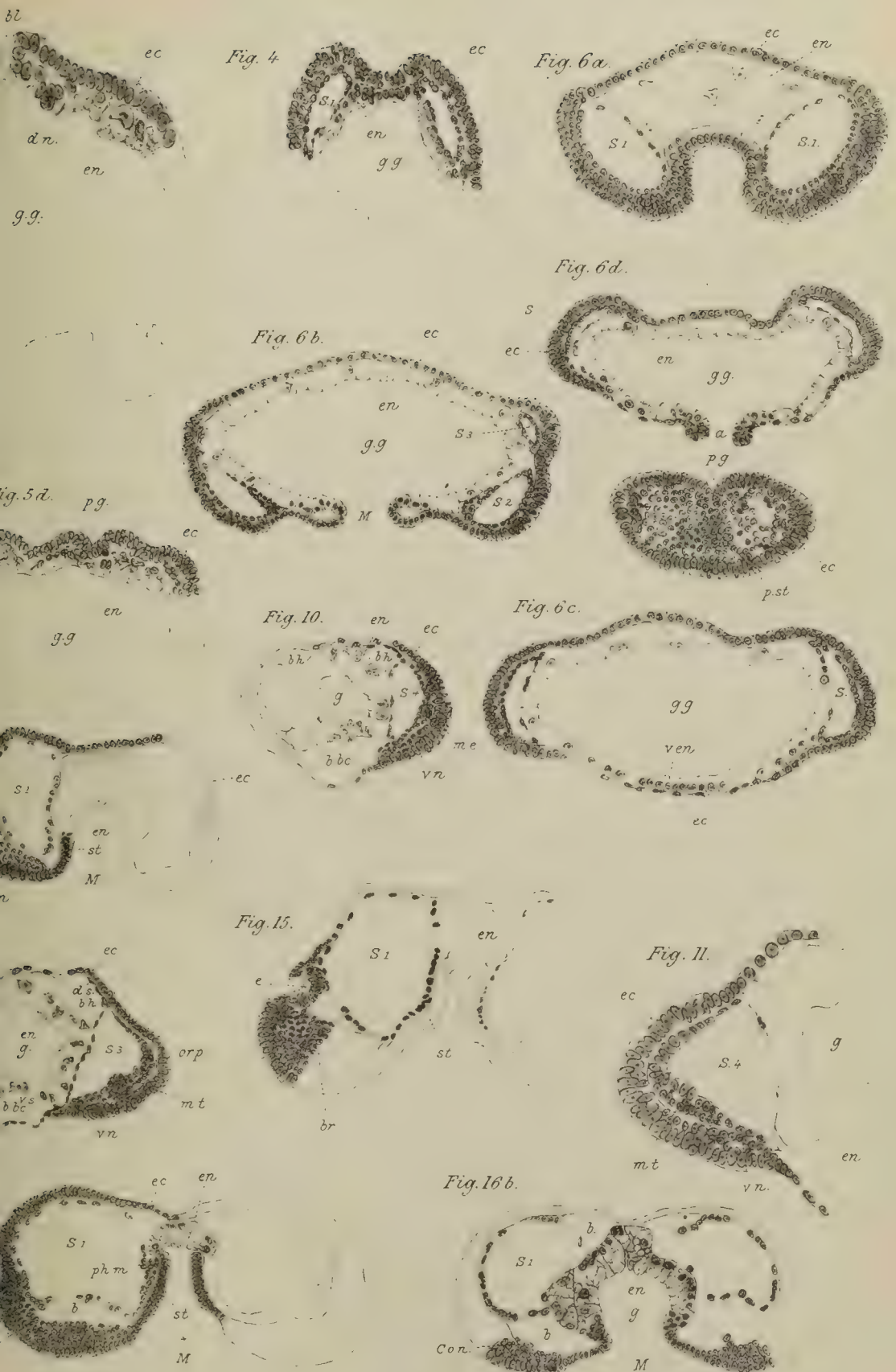








Fig. 17a

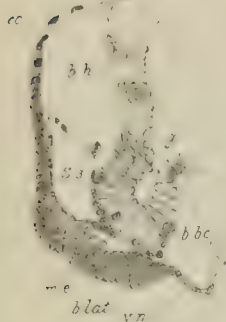


Fig. 17b



Fig. 17c



Fig. 18a

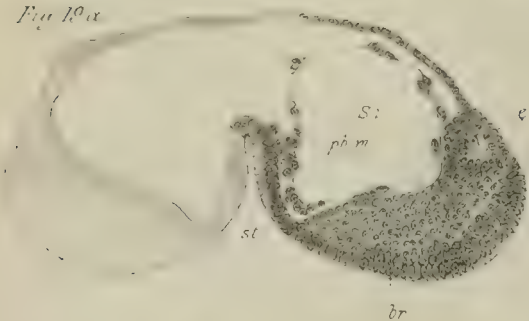


Fig. 21



Fig. 19b

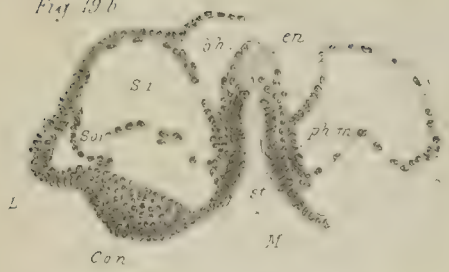


Fig. 22a

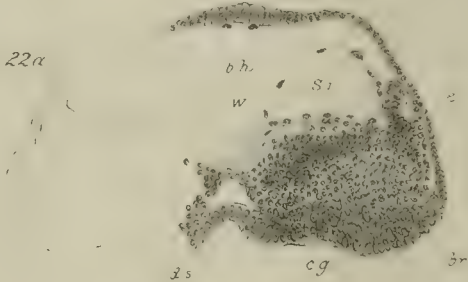


Fig. 23a

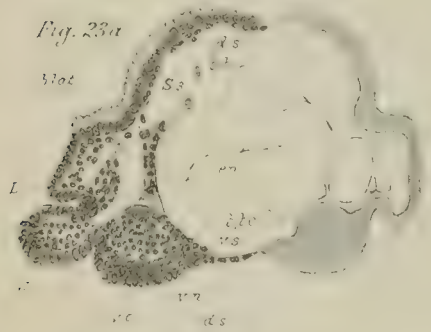


Fig. 23c

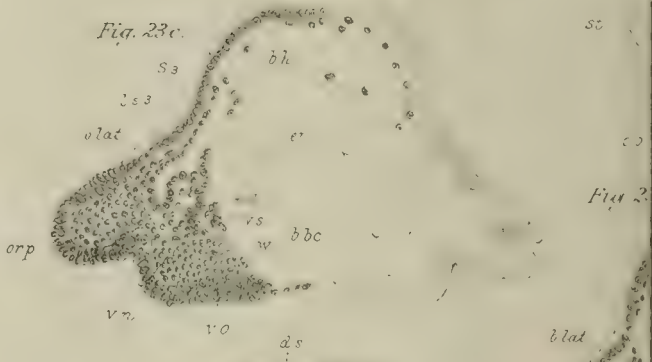
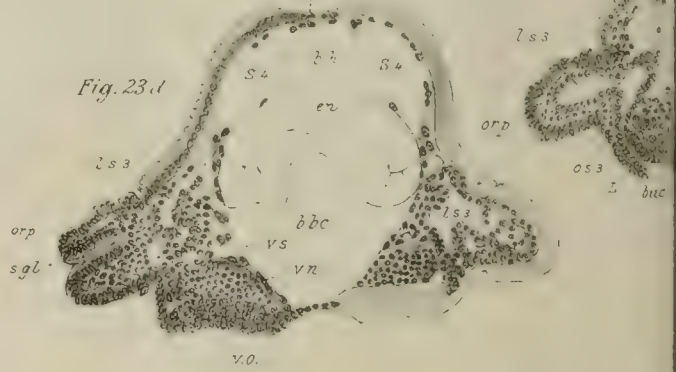


Fig. 23b



Fig. 23d



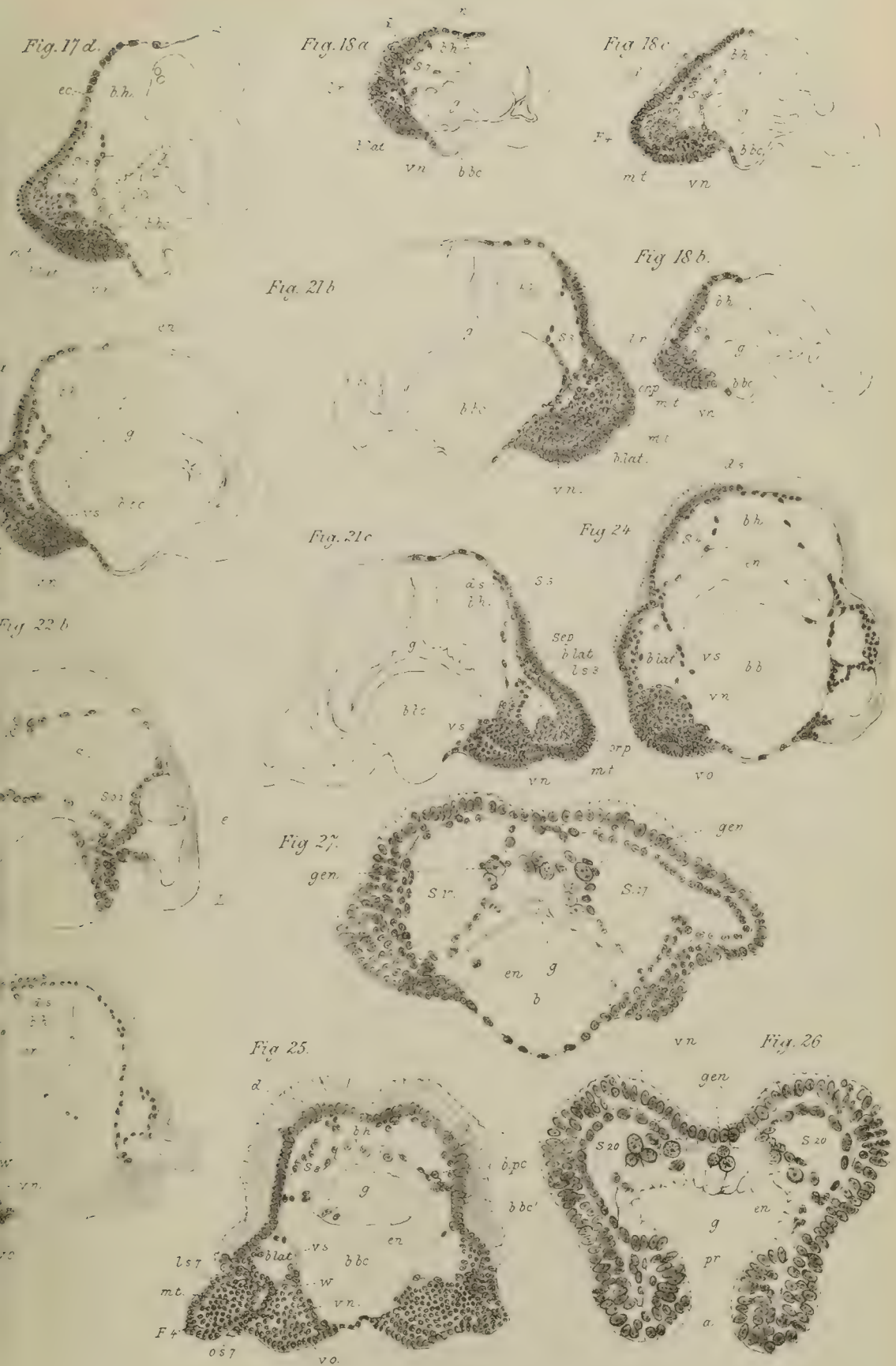








Fig. 28



Fig. 31

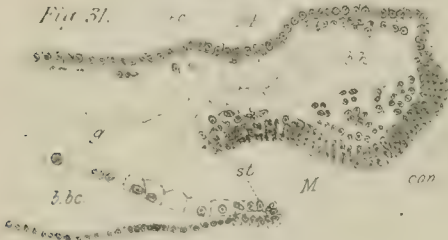


Fig. 32



Fig. 33



Fig. 34

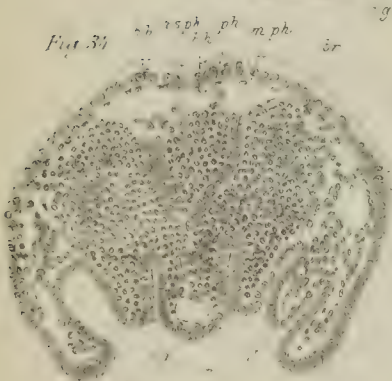


Fig. 36

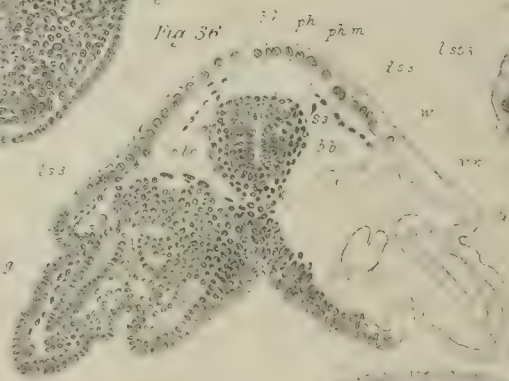


Fig. 38



Fig. 35

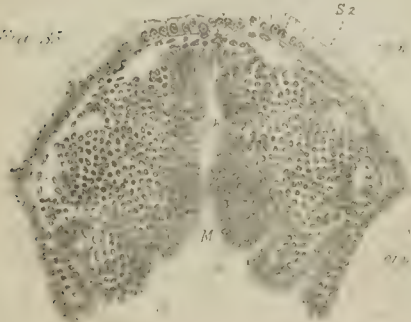


Fig. 37

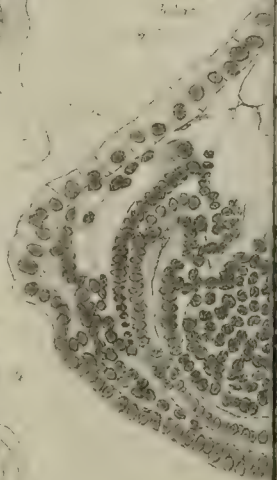








Fig 42.

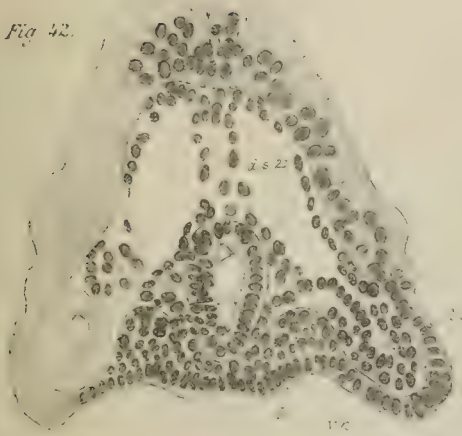


Fig 43

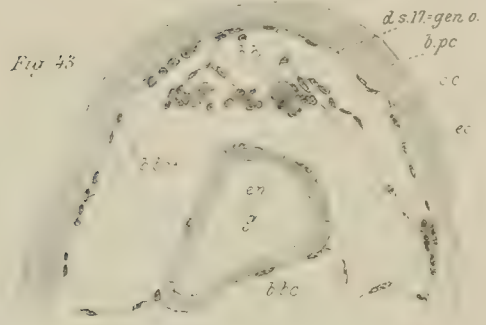


Fig 40



Fig 44

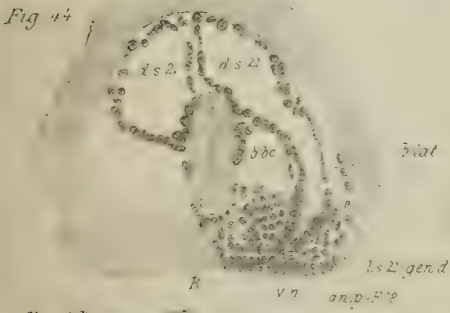


Fig 45

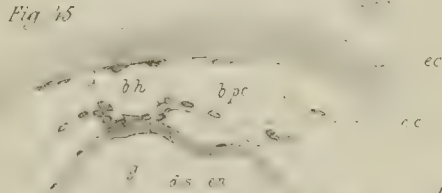


Fig 47

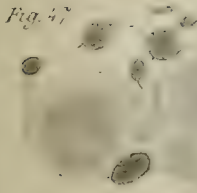


Fig 48

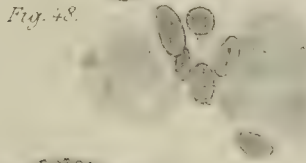


Fig 51



Fig 49



Fig 50

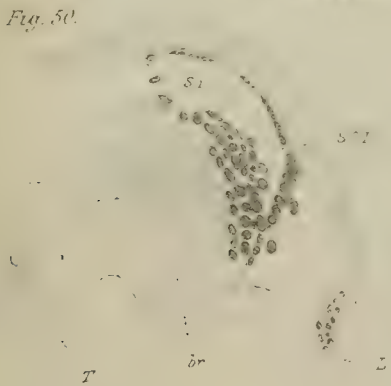


Fig 52

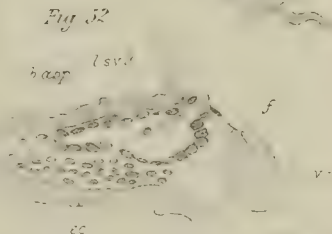


Fig 53a

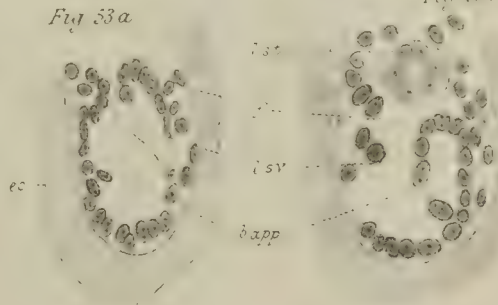


Fig 53b





## EXPLANATION OF PLATES X, XI, XII, and XIII,

### *List of Reference Letters.*

*a.* Dorso-lateral horn of white matter of brain. *b.* Ventro-lateral horn of white matter of brain. *b. app.* Body cavity of appendage, a blood-space. *b. lat.* Lateral compartment of body cavity (space formed in parietal mesoderm); a blood-space. *cer. ves.* Cerebral vesicles or ventral appendages of brain. *circ. musc.* Circular muscles of body wall. *crur. gl.* Rudiment of crural gland. *E.* Central lobe of white matter of brain. *l. s. t. 3.* Tubular part of nephridium of third somite. *l. s. v. 3.* Internal vesicle of nephridium of third somite. *neuro-musc.* Network of fibres, so-called because it gives rise to nerves and muscles; it is continuous with the lateral pedal nerve, and is apparently composed of a substance like the latter and the white matter of the cord. It is derived from a compact mass of nuclei present in the previous stages at the same point. *or. pap.* Oral papilla. *o. s. 3.* External opening of nephridium of the third somite. *sal. gl.* Salivary gland, *sl. gl.* Slime-gland. *v. o.* Ventral organ. *v. o. 1.* Ventral organ of jaws. *v. s.* Septum separating the central from the lateral compartments of the body cavity, called in earlier stages the ventral sheet of somatic mesoderm.

FIGS. 1—4.—A series of transverse sections through the head of an embryo of *Peripatus Balfourii* of Stage G (removed from the uterus on 12th December). One side only of each section is completely drawn. The dorsal ectoderm possesses a large number of highly refractile spheres, probably yolk-spheres, and has contracted on to the brain so as to render indistinct the mesoderm structures between. *a.* Dorso-lateral. *b.* Ventro-lateral. *c.* Central lobe of white matter.

Fig. 1. Through the region of the eye and anterior lobes of the brain. One side only is figured, and the nuclei of the ventral part of the brain are omitted. The section goes through the optic nerve and centre of the optic vesicle. Zeiss's camera, obj. D, oc. 2.

Fig. 2. A little farther back, through the anterior part of the cerebral vesicle (*cer. ves.*) and the region of junction of the two halves of the brain. The dorsal mass of nuclei and the central lobe of white matter have united with the corresponding structures of the opposite side. Ventrally the two halves of the brain are separate.

Fig. 3. A little farther back, through the centre of the cerebral vesicles, and still through the joined part. The dorsal mass of nuclei are absent, and the white matter is broadly exposed dorsally.

Fig. 4. Through the posterior lobes of the brain and the region of the buccal cavity. The ventral organ of the jaw (*v. o. 1*) and the jaw are

## EXPLANATION OF PLATES X AND XI.

shown. The oral papilla (*or. pap.*) and slime-gland (*sl. gl.*) are also visible.

Figs. 2—4 drawn with Zeiss's camera, obj. C, oc. 2.

FIG. 5.—Portion of transverse section through the middle region of the body of an embryo of *Peripatus capensis* of Stage G (removed from uterus 16th December). The section passes through the anterior part of a pair of legs. The details are filled in on the left-hand side of the drawing. The section passes through a ventral organ (*v. o.*), with which the nerve-cords are connected by a cellular process, a persistent trace of the original complete continuity between these two structures. The anterior of the two large pedal nerves is shown (*nerve*), leaving the cord as it immediately passes forwards out of the plane of the section; the continuity between it and the neuro-muscular network (*neuro-musc.*), which will eventually develop into the nerves and muscles of the foot, and between it and the circularly disposed network from which the circular muscles (*circ. musc.*) of the body wall will develop, could not be shown in this figure. The walls of the alimentary canal are very thin. *b. lat.* marks the lateral compartment of the vascular body cavity (space formed in parietal mesoderm of early stages). *b. app.* The vascular body cavity of the appendage. Drawn on the table, Zeiss's new camera C, oc. 2.

FIG. 6.—A diagram of the ventral portion of the third somite at Stage F. The vertical lines indicate the planes of the sections Figs. 37, 38, 39 of Part III.

FIG. 7.—Diagram of the ventral portion (nephridium) of third somite at birth. The hinder part of the tube of the preceding stage has elongated backwards to form the long tubular salivary gland (*sal. gl.*).

FIGS. 8—13 are all from embryos just before birth (removed from uterus 19th April). They were all drawn on the table with a Zeiss's new camera, obj. C, oc. 2.

Figs. 8 and 9. Transverse sections through the same structure, along the lines marked 8 and 9 in the preceding diagram (Fig. 7). The vesicle (*l. s. v. 3*) has thick, much vacuolated walls, and is placed dorsal to the tubular part (*l. s. t. 3*). In Fig. 9, the small portion connecting the vesicle and tube is shown closely applied to the dorsal wall of the salivary gland.

FIG. 10. Portion of a transverse section through the region of the third leg of *P. capensis* just before birth. The section passes through the opening of the nephridium, and what I take to be the rudiment of the crural gland (*crur. gl.*). The whole nephridium is shown in the section. In the actual section the internal vesicle was somewhat more collapsed than in the figure. The funnel and internal vesicle I take to be homologous with the similarly named structures of the posterior nephridia.



## EXPLANATION OF PLATES XI AND XII.

Fig. 11. Portion of a transverse section through the region of one of the posterior legs of *P. capensis* just before birth. The section passes through the opening of the nephridium and the rudimentary crural gland. The tubular part of the nephridium is cut in two places, and its terminal portion with the closely-packed nuclei is shown opening into the internal vesicle. The cavity of the leg is traversed by a considerable amount of muscular tissue external to the nephridium, and contains some of the reticular tissue in its dorsal part. The septum separating the lateral sinus from the leg cavity is absent in this region.

Fig. 12. Section through the ovaries of an embryo of *P. capensis* just before birth. On the right side there is an attachment to the pericardium. The dark elongated nuclei are follicular nuclei.

Fig. 13. Dorsal part of a transverse section of a male of *P. capensis* just before birth. In most embryos of this age the wall of the heart is separate (always connected by filaments) from the dorsal body wall and the pericardial floor. The apparent fusion in this section was probably due to contraction of the body. The two patches of dorsal longitudinal muscles are shown.

FIGS. 14—17 are a series of diagrams to show the relations of the coelom and body cavity at successive stages. The lining of the coelom is shaded dark, the light shading indicates the general mesoderm.

Fig. 14. Earliest stage: coelom as a series of separate spaces. The ectoderm and endoderm still in contact: no trace of the vascular space or hæmocœle.

Fig. 14*a*. The endoderm has already separated from the dorsal and ventral ectoderm. On the right-hand side the somite has not yet divided into a dorsal and ventral portion. The first rudiment of the lateral sinus is present in the thickened mesoderm. On the left side the coelom has divided into a dorsal part, which in the anterior part of the body vanishes, but in the posterior part becomes the generative organ; and into a ventral part which becomes a nephridium. The lateral sinus has increased in size, and a space has appeared in the mesoderm of the leg.

Fig. 15. The dorsal division of the coelom has passed dorsalwards, and considerably encroached upon the dorsal of the two blood-spaces formed by the separation of the endoderm and ectoderm. This median dorsal blood-space becomes the heart. Two spaces have appeared in the ventral wall of the dorsal division of the somites; the dorsal of these becomes the pericardium, the ventral the dorsal part of the central compartment of the body cavity. The ventral blood-spaces have increased in size, but are otherwise unchanged.

Fig. 16. The dorsal divisions of the somites have relatively diminished in size, and been overlapped dorsally by the greatly increased pericardium.

### EXPLANATION OF PLATE XIII.

The dorsal part of the central compartment of the body cavity has increased in size, but is still separated ventrally by a septum. The ventral blood-spaces have increased in size. The ventral division of the coelom is assuming the form of a nephridium.

Fig. 17. Diagram of arrangement at birth. The two halves of the pericardial cavity have coalesced dorsally and ventrally to the median-dorsal blood-space which forms the heart. The dorsal divisions of the coelom have become constricted off from the floor of the pericardium and the dorsal wall of the enteron, and now lie in the central compartment of the body-cavity and constitute the generative tubes (in the anterior part of the body they atrophy in the floor of the pericardium). The horizontal septum separating the dorsal division of the central compartment of the body cavity from the ventral has vanished. The ventral or nephridial division of the coelom has assumed the form of a nephridium. On the left hand the whole course of the nephridium is diagrammatically shown.



Fig. 3



Fig. 4.



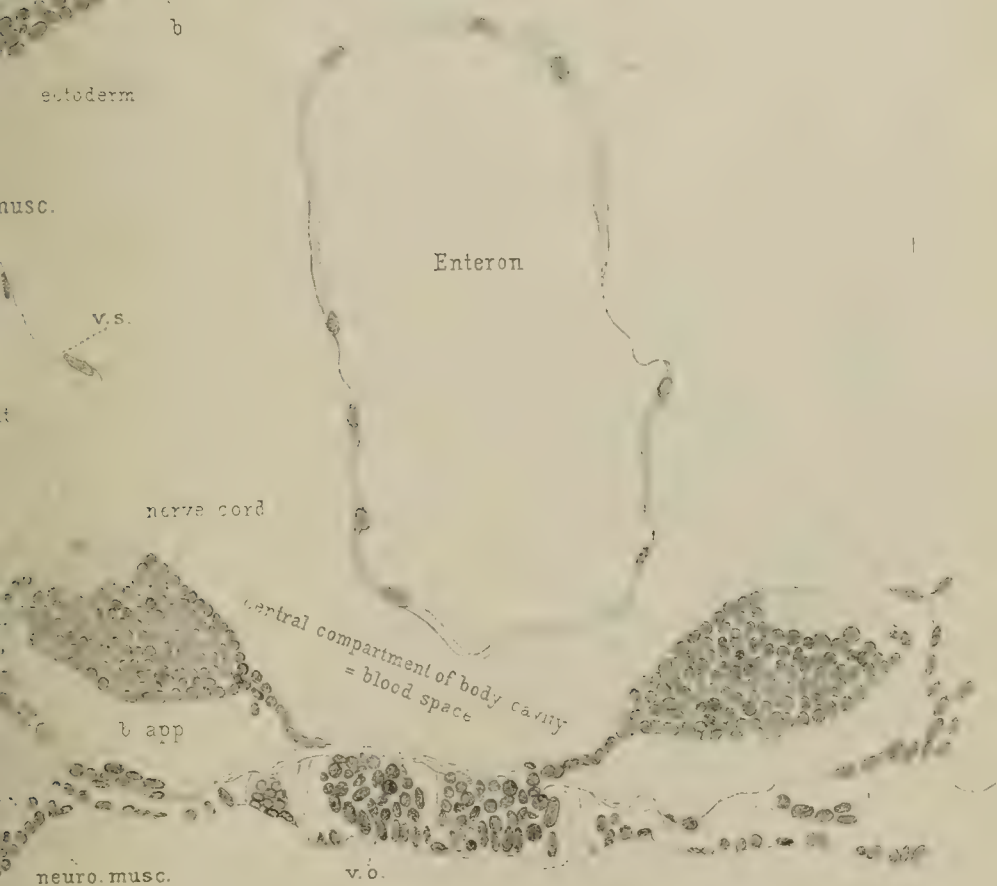
Fig. 5.



Fig. 1.

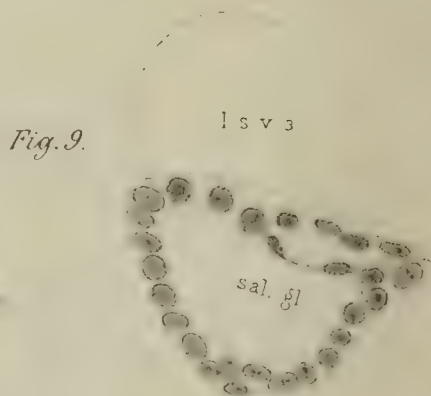
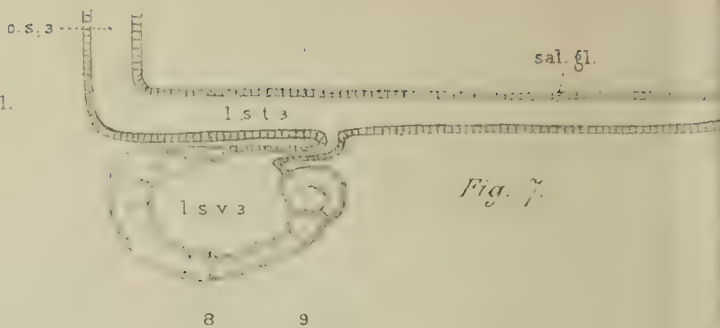
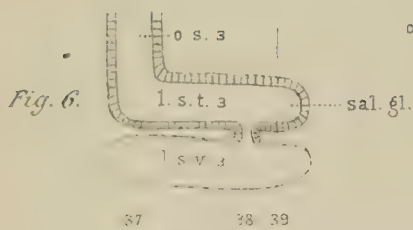


Fig. 3.









*Fig. 12.* floor of pericardium

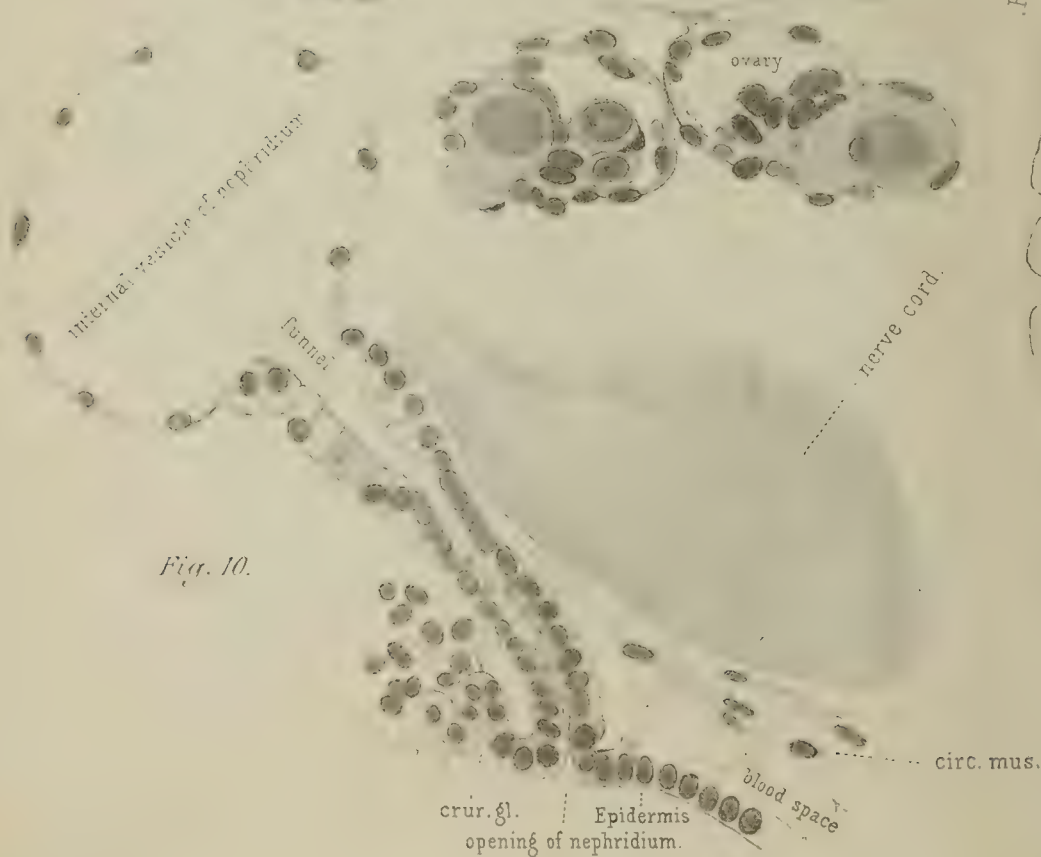




Fig. 11.





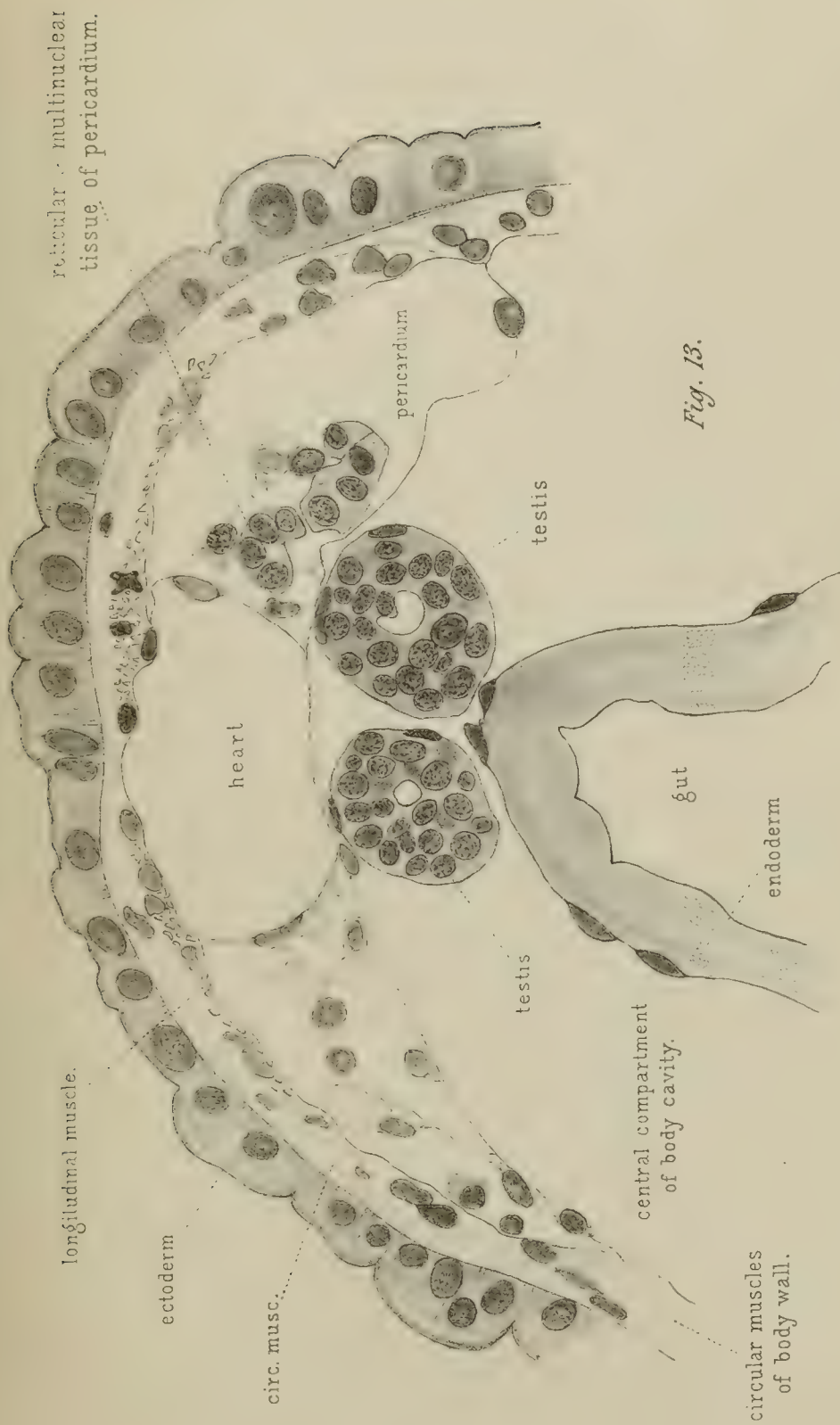


Fig. 13.







Vol. 14.

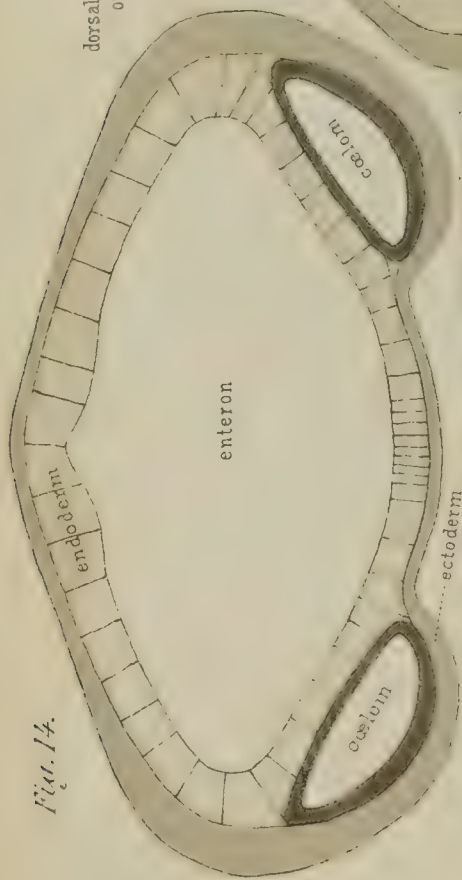


Fig. 16.

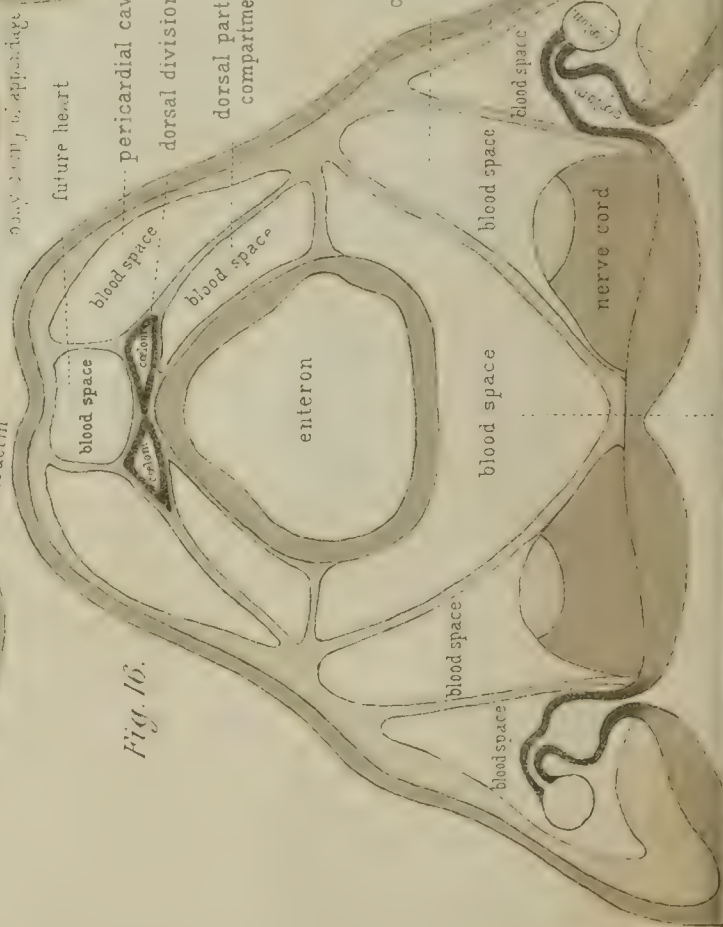


Fig. 14a.

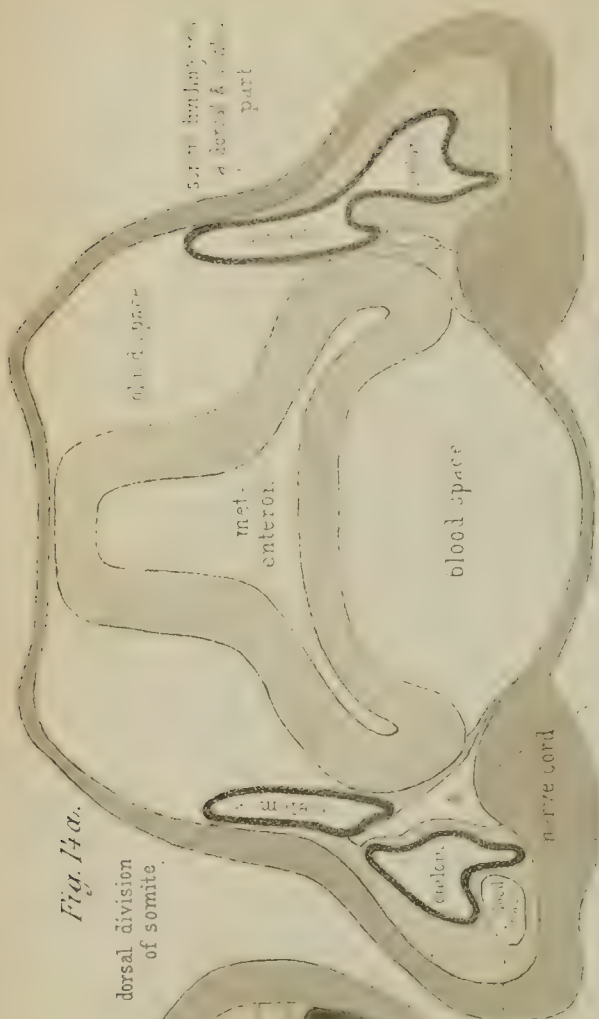
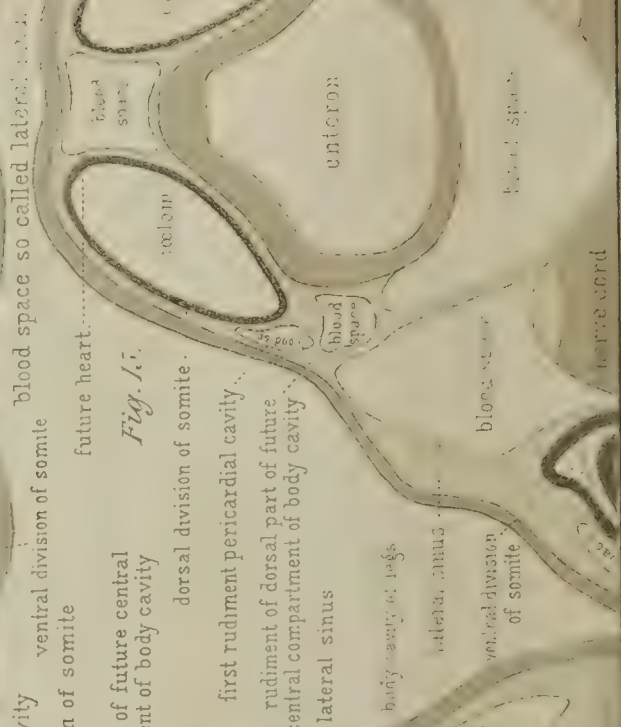
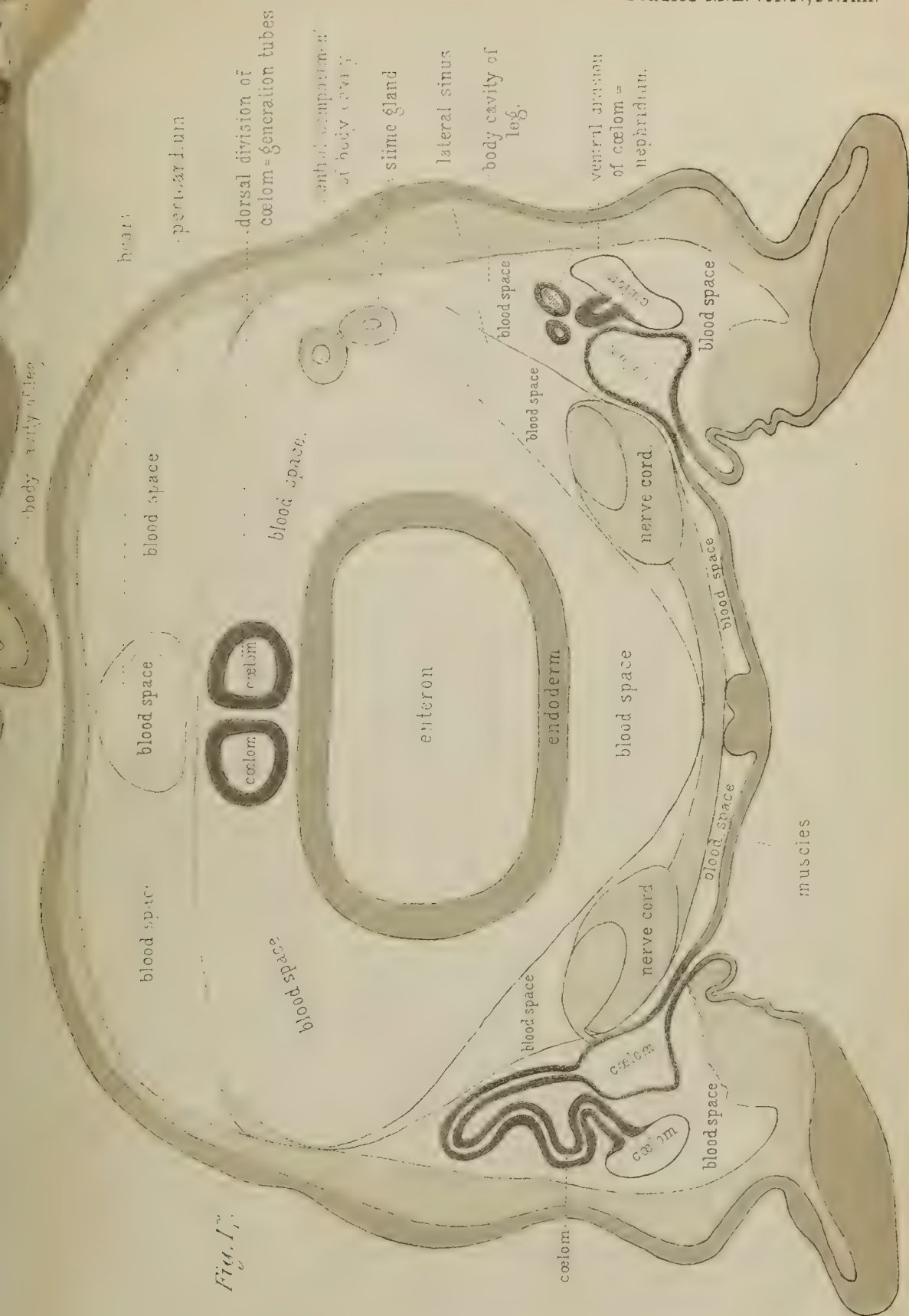


Fig. 15.





FILE





A MONOGRAPH  
OF  
THE SPECIES AND DISTRIBUTION  
OF THE  
GENUS PERIPATUS

BY  
ADAM SEDGWICK, M.A., F.R.S.

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# THE GENUS PERIPATUS.

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## INTRODUCTION.

THE editors of the posthumous memoir of Professor F. M. Balfour on the anatomy and development of *Peripatus capensis* stated, in a note at the end of the memoir, their intention of preparing a complete monograph of the known species of *Peripatus*. This intention has at length been carried out, and the present monograph is the result of a laborious examination of all the specimens of *Peripatus* to which it has been possible to get access.

To my great regret Professor Moseley has been obliged, by his most unfortunate illness, to withdraw from active participation in the work; and the whole responsibility for the statements and descriptions falls upon me alone. But he has given me much valuable assistance, and has made some substantial contributions to the monograph. The most important of the latter relate to *Peripatus novæ-zealandiæ*. He examined this species with great care, and the drawings from which figs. 16, 17—20, and 30 were copied, were executed under his supervision.

The material at my disposal has been as follows:

1. The material left by Professor Balfour. This comprised a large number of the Cape species collected by Mr. Lloyd Morgan and by the late Mr. Oakley of the South African Museum, and some specimens of the New Zealand species collected by Professor Moseley and Professor Jeffrey Parker. Balfour also had fourteen specimens from Caracas, sent him, I believe, by Professor Ernst, and one specimen from South Africa, of the exact locality of which I am ignorant, with twenty-two pairs of legs. This specimen was found by Mr. Mansel Weale, and given to Balfour by Mr. Wood Mason.

2. A large number of specimens from the Cape, collected partly by myself in 1883, and brought to England alive, and partly by Mr. C. Stewart, of the Royal Hotel, Wynberg, who in the winters of 1884-85 sent me a large additional supply of live animals collected on Table Mountain. I am under great obligations to Mr. Stewart, not only for these specimens, but for the great help which he gave me when I was at the Cape.

3. A large number of living specimens from Wellington, New Zealand. These are the only specimens of this species which have ever been brought to England alive, and I owe them to the kindness of two gentlemen, who were personally unknown to me until they began to help me in my *Peripatus* work. Mr. Noel Barraud, of Wellington, at the request of my friend Mr. G. E. Anson, M.A., of Trinity College, began to hunt for *Peripatus*, and was successful in finding them. His specimens were, after two unsuccessful attempts, brought to England alive by Mr. Edgar J. Evans, chief officer of the Shaw, Savill, Albion Company's magnificent steamer "*Tainui*." The first two lots all died soon after leaving Rio Janeiro, but in the third attempt Mr. Evans was successful in finding a place near the cold chamber, where the temperature in the tropics was not too high for the animals. Since the third attempt Mr. Evans has been successful every voyage. My most sincere thanks are owing to both of these gentlemen, who, though not specially interested in natural history, have put themselves to very considerable trouble and inconvenience to satisfy what would have seemed to most people an absurd whim of a perfect stranger. The living animals brought by Mr. Evans have enabled me to give a much more complete account of the New Zealand species than if I had had to rely only on the somewhat shrunk and contracted specimens in Balfour's material; and the embryos found in them are now being used by Miss Sheldon (No. 45), of Newnham College, who is engaged in preparing a memoir of their development.

4. Several specimens of the neotropical group of species from the Museum of Copenhagen, most kindly sent to me by

Professor Steenstrup, in response to the appeal for specimens at the end of Balfour's posthumous memoir.

5. Dr. J. Kennel, of Würzburg, was kind enough to send me, in exchange for two living specimens of *Capensis*, two specimens of the smaller species, which he found in Trinidad.

6. Four specimens from near Williamstown, South Africa, belonging to the Indian Museum.

7. All the specimens in the British Museum. These have not, unfortunately, been of so much use to me as I had hoped, on account of their small number and contracted condition, and of the difficulty of getting a sufficiently strong light in the rooms set apart for the examination of spirit specimens in the British Museum, for the minute examination which is required. I am greatly indebted to Professor Jeffrey Bell, of the British Museum, for his courtesy in giving me every facility in his power to examine the specimens.

8. Two specimens from Queensland, Australia, belonging to Professor Jeffrey Bell. He has been most kind in putting them entirely at my disposal for the purposes of this monograph.

9. About twenty specimens from Demerara, brought alive to England by Mr. W. L. Sclater. Mr. Sclater has himself given a short description of these specimens, and has kindly placed the greater number of them at my disposal for the purposes of this monograph. These specimens were all killed and opened by me shortly after their arrival in order that their embryos might be cut out and preserved. The result is that they are somewhat contracted and not so favorable for observation as they would have been had they been drowned.

Of the figures illustrating this monograph, the beautiful drawings of *Capensis* on Pl. XV, of *Edwardsii*, *Moseleyi*, and *Novæ-zealandiæ* on Pl. XVII, were made by Miss A. B. Balfour in Professor Balfour's lifetime and under his direction. The figures on Pl. XVI were made by Miss Balfour after her brother's death. To enable me to complete

the illustrations required and to assist in the publication of the monograph, the Government Grant Committee of the Royal Society granted the sum of £50. Figs. 16, 17—20, and 30 were made at Oxford by Mr. W. H. Hill, under Professor Moseley's direction and supervision. The remainder of the drawings, including that of the living animal of Pl. XIV, were made by Mr. E. Wilson, of the Cambridge Scientific Instrument Company. My best thanks are due to these gentlemen for the care and skill with which they have executed their work.

Finally, I have again to acknowledge my indebtedness to Professor Jeffrey Bell for his assistance in preparing the Bibliography. Several papers which had escaped my notice were first pointed out to me by him.

For an account of the general anatomy and characters of the genus *Peripatus*, I must refer to the memoirs of Moseley (No. 18), Balfour (No. 28), and Gaffron (Nos. 34, 35). In this monograph only those features of a specific differential value are dwelt upon. I have, however, made a partial exception to this rule in the case of *Capensis*, the external characters of which have been described at considerable length. The reader will be able to gather from this description a sufficient knowledge of the general external features of the genus to enable him to understand the short descriptions of the other species.

The chief result of my observations has been to establish a definite series of characters which distinguish quite sharply all the species found in one region of distribution from those found in the others. Excluding the doubtful case of the Sumatran species, *Peripatus* has been found in the Ethiopian region (South Africa), the Australasian, and the Neotropical regions, and in each of these regions the genus is represented by more than one species. I have been able to establish a certain number of new species, but on the whole I must confess to failure in this respect. My failure chiefly relates to the species from the Neotropical region, and is due to the insufficient



number of specimens at my disposal. It is remarkable of the species from this region that the number of the walking legs varies considerably within the same species, and it is only possible to determine the limits of the variation by examining a large number of individuals. Inasmuch as the specific characters other than those afforded by the legs are extremely inconspicuous, the importance of having a large and well preserved material is obvious—large in numbers to enable one to establish the limits of leg variation, and well preserved that the more minute specific differences may be made out.

How inconspicuous the specific characters are is well shown by contrasting the South African species *Capensis* and *Balfouri*. That these are distinct species is proved by the fact that the number of legs is constant in all the large number of specimens examined, and by the fact that it is preserved in the reproduction of the species. Embryos removed from *P. capensis* have invariably seventeen pairs of legs, while embryos removed from *P. Balfouri* have invariably eighteen pairs. The other differences relate simply to the texture and tint of the skin, and are so minute as to escape any but the experienced eye.

Before concluding this introduction, I am desirous of pointing out how extremely loose and inaccurate have been the observations of some professed zoologists on the members of our genus. In several cases has it happened that the observer (*sit venia verbo*) has not been at the trouble of counting the legs of his specimens, though he has not refrained from making statements on this point, and in more than one case the number of legs in the specimen figured does not correspond with the author's statement in the text. If one may draw conclusions as to these zoologists' ideas of accuracy in observation from such instances in which only the most obvious external features are concerned, one would be inclined to infer that but little value can be attached to their statements with regard to the more inconspicuous details, which require some nicety of observation.

## CHAPTER I.

### THE GENUS **PERIPATUS** Guilding.

Soft-bodied vermiform animals, with one pair of ringed antennæ, one pair of jaws, one pair of oral papillæ, and a varying number of claw-bearing ambulatory legs. Dorsal surface arched and more darkly pigmented than the flat ventral surface. Skin transversely ridged and beset by wart-like spiniferous papillæ. Mouth anterior, ventral; anus posterior, terminal. Generative opening single, median, ventral, and posterior. One pair of simple eyes. Brain large, with two ventral hollow appendages; ventral cords widely divaricated, without distinct ganglia. Alimentary canal simple, uncoiled. Segmentally arranged, paired nephridia are present. Body cavity is continuous with the vascular system, and does not communicate with the paired nephridia. Heart tubular, with paired ostia. Respiration by means of tracheæ. Diœcious; males smaller and generally less numerous than females. Generative glands tubular, continuous with the ducts. Viviparous. Young born fully developed. They shun the light, and live in damp places beneath stones, leaves, and bark of rotten stumps. They eject when irritated a viscid fluid through openings at the apex of the oral papillæ.

Distribution: South Africa, New Zealand, and Australia, South America and the West Indies [and Sumatra?].

The genus *Peripatus* was established in 1826 by Guilding (No. 1), who first obtained specimens of it from St. Vincent in the Antilles. He regarded it as a Mollusc, being no doubt deceived by the slug-like appearance given by the

antennæ. Specimens were subsequently obtained from other parts of the Neotropical region and from South Africa, and the animal was variously assigned by the zoologists of the day to the Annelida and Myriapoda (vide Moseley, No 22, and Selater, No. 41). Its true place in the system, as a primitive member of the group Arthropoda, was first established in 1874 by Moseley (No. 18), who discovered the tracheæ. It was reported from Australia in 1869 by Saenger (No. 15), and from New Zealand by Hutton (No. 19) in 1876. The nephridia were first discovered by Saenger (No. 15), but they were re-discovered and more fully described by Balfour (Nos. 21 and 28). Gaffron was the first to observe the cardiac ostia and the cilia in the generative tracts. The development has been worked at by Moseley (No. 18), Hutton (No. 19), Balfour (No. 28), and more in detail by Kennel (Nos. 32 and 33), Sheldon (No. 45), Selater (No. 46), and myself (No. 39).

There can be no doubt that *Peripatus* is an Arthropod, for it possesses the following features, all characteristic of that group, and all of first-class morphological importance. (1) The presence of appendages modified as jaws. (2) The presence of paired lateral ostia perforating the wall of the heart and putting its cavity in communication with the pericardium. The importance of this feature as an Arthropod character was first pointed out by Lankester. (3) The presence of a vascular body cavity and pericardium (hæmocœlic body cavity). (4) The inconspicuous character of the cœlom in the adult. Finally, the tracheæ, though not characteristic of all the classes of the Arthropoda, are found nowhere outside that group, and constitute a very important additional reason for uniting *Peripatus* with it.

*Peripatus*, though indubitably an Arthropod, differs in such important respects from all the old-established Arthropod classes, that a special class, equivalent in rank to the others, and called *Prototracheata*, has had to be created for its sole occupancy. This unlikeness to other Arthropoda is mainly due to the Annelidan affinities which it presents, but in part to the presence of the following peculiar features: (1) the number and diffusion of the tracheal apertures, (2) the restriction

of the jaws to a single pair, (3) the disposition of the generative organs, (4) the texture of the skin, and (5) the simplicity and similarity of all the segments of the body behind the head.

The Annelidan affinities are superficially indicated in so marked a manner by the thinness of the cuticle, the dermo-muscular body wall, the hollow appendages, that, as already stated, many of the earlier zoologists who examined *Peripatus* placed it amongst the segmented worms; and the discovery that there is some solid morphological basis for this determination constitutes one of the most interesting points of the recent work on the genus. The Annelidan features are: (1) the paired nephridia in every segment of the body behind the first two (Sacnger, Balfour), (2) the presence of cilia in the generative tracts (Gaffron). It is true that neither of these features are absolutely distinctive of the Annelida, but when taken in conjunction with the Annelid disposition of the chief systems of organs, viz. the central nervous system, and the main vascular trunk or heart, may be considered as indicating affinities in that direction. *Peripatus*, therefore, is zoologically of extreme interest from the fact that, though in the main Arthropodan, it possesses features which are possessed by no other Arthropod, and which connect it to the group to which the Arthropoda are in the general plan of their organisation most closely related. It must, therefore, according to our present lights, be regarded as a very primitive form; and this view of it is borne out by its extreme isolation at the present day. *Peripatus* stands absolutely alone as a kind of half-way animal between the Arthropoda and Annelida. There is no gradation of structure within the genus; the species are very limited in number, and in all of them the peculiar features above mentioned are equally sharply marked.

We may, therefore, with some justice, regard *Peripatus* as an animal which has persisted for a long time, with but little structural modifications; as the representative of an ancient group, once widely diffused,<sup>1</sup> and probably rich in species and

<sup>1</sup> That the class had once a world-wide diffusion is indicated by the wide and discontinuous distribution of the living species.



genera, and closely related to the ancestors of living Arthropoda. It probably has owed its preservation, as so many of the survivals of ancient types seem to have done, to the peculiar habits of life which are shared by all the living members of the class, viz. the habitual avoidance of the light of day, and the habit of seeking the obscurity and protection afforded by the spaces beneath stones and beneath the bark of trees.

*Peripatus*, though a lowly organised animal, and of remarkable sluggishness, with but slight development of the higher organs of sense, with eyes the only function of which is to enable it to avoid the light—though related to those animals most repulsive to the æsthetic sense of man, animals which crawl upon their bellies and spit at, or poison, their prey—is yet, strange to say, an animal of striking beauty. The exquisite sensitiveness and constantly changing form of the antennæ, the well-rounded plump body, the eyes set like small diamonds on the sides of the head, the delicate feet, and, above all, the rich colouring and velvety texture of the skin, all combine to give these animals an aspect of quite exceptional beauty. Of all the species which I have seen alive, the most beautiful are the dark green individuals of *Capensis*, and the species which I have called *Balfouri*. These animals, so far as skin is concerned, are not surpassed in the animal kingdom. The drawing on Pl. XIV, is from one of the dark green specimens of *Capensis*. Clever as the drawing is, the artist has failed to catch the exquisite velvet of the skin; but this could hardly be expected in a lithograph. I never shall forget my astonishment and delight when on bearing away the bark of a rotten tree-stump in the forest on Table Mountain, I first came upon one of these animals in its natural haunts, or when Mr. Trimen showed me in confinement at the South African Museum a fine fat, full-grown female, accompanied by her large family of thirty or more just-born but pretty young, some of which were luxuriously creeping about on the beautiful skin of their mother's back.

## CHAPTER II.

### THE SOUTH AFRICAN SPECIES OF PERIPATUS.

The following is a list of the distinct species of *Peripatus* which have so far been found in South Africa: *Capensis* (Table Mountain), *Balfouri* (Table Mountain), *brevis* (Table Mountain), *Moseleyi* (near Williamstown). In addition to these there are a certain number of other possible species, concerning the distinctness of which, however, I cannot be certain.

### General Characters of the South African *Peripatus*.

*Peripatus* with three spinous pads on the legs, with two primary papillæ on the anterior side of the foot (fig. 2), and a small tooth at the base of the main tooth on the outer blade of the jaw (fig. 28). The last fully developed leg of the males is provided with a white papilla on its ventral surface (fig. 4), and an enlarged crural gland. The generative opening is always subterminal and behind the last pair of fully developed legs. The ovaries are attached to the floor of the pericardium by a ligament which passes off from their front end. The terminal unpaired portion of the vas deferens of the male is short. The ova are large, but with little food-yolk. The portion of the proximal pad of the fourth and fifth legs, which carries the opening of the nephridium, is separated by faintly marked grooves from the rest of the pad (fig. 9). The legs appear, with rare doubtful exceptions, to be constant in number in all specimens of the same species. The median line of the dorsal surface is destitute of pigment. The blastopore of the gastrula stage gives rise to the mouth and anus of the adult.

*Peripatus capensis* being the best known and the most easily procured will be taken as the type of this group of species.

**Peripatus capensis.**

*South African Peripatus with seventeen pairs of claw-bearing ambulatory legs.*

The females are, on the whole, larger than the males, but the difference between them is not very marked. A large female would measure about 65 mm. ( $2\frac{1}{2}$  inches), and a large male about 48 mm. There are, however, other external differences between the sexes. The last leg of the male is smaller than the preceding, and rarely touches the ground when the animal is walking, while in the female it is as large as the others, and used in walking. Further, the last leg of the male possesses, on its ventral surface, a small white papilla (fig. 4), at the apex of which opens its crural gland, which is much enlarged.

In the living animal (Pl. XIV) the skin has a beautiful velvety texture. This is especially noticeable in the darker specimens.

**Colour.**—The colour varies in different individuals. But in general it may be said that the ventral surface has a light colour, and that the dorsal is darkly pigmented. The principal colours are two in number, which present every variation in tint in different individuals and in different parts of the body of the same individual. They are (1) a dark green, graduating to a bluish grey; (2) a brown, varying to a red orange.

The ventral surface is almost entirely free from the green pigment, but possesses a certain amount of light brown. This brown pigment is more conspicuous and of a darker shade on the spinous pads of the legs. The only part of the ventral surface where the green pigment is always present is the ventral side of the foot, where it has a blue tint, and round the lips (fig. 5). In the latter situation there are a number of green papillæ, with which are intermingled a few of an orange colour. Very rarely there is a suspicion of green pigment along the middle line of the ventral surface, and in one specimen I found the distal pad of the leg to contain green pigment.

While the colour of the ventral surface is practically the same in all individuals, that of the dorsal differs in almost all. The differences are due to the varying proportions in which the green and brown pigments are present.

To facilitate matters I will describe two extreme cases: (1) a very dark green specimen (fig. 1), in which the brown is very inconspicuous, and (2) a red specimen, in which the brown predominates.

(1) The skin between the close-set papillæ, so far as it can be observed, is a bluish grey; but on the papillæ the pigment has a very dark green colour, except on a few, in which it is brown (even these may be absent). The ground colour, i.e. the colour of the skin between the papillæ, varies in shade in different places. On the dorsal sides of the legs and along a dorso-lateral band at the bases of the legs, extending the whole length of the body, it is lighter than elsewhere, while on each side of the median dorsal white line it is much darker than elsewhere. These differences may be partly due to the closer aggregation of the papillæ in one place than in the other.

(2) The pigment of the skin and of most of the papillæ is a reddish brown, except on each side of the dorsal white line and on the dorsal sides of the legs where it is green. Scattered amongst the brown papillæ are a considerable number of green. The brown colour is of a lighter shade along a dorso-lateral band, extending the whole length of the body at the base of the legs, and from this band green papillæ are almost entirely absent. The brown pigment is, however, almost entirely absent from the dorsal side of the legs on each side of the dorsal white line.

The conditions intermediate between these two extreme cases are due to the variations in the number of the brown papillæ. As a peculiarity of these intermediate cases may be mentioned the fact that the brown pigment extends into the skin round the base of the brown papillæ, giving the brown papillæ a brown setting, so that when a number of them occur together the skin between the papillæ has an entirely brown colour (as in the brown specimens). Brown papillæ are most numerous in the light band at the bases of the legs, and are



sometimes so numerous that the ground colour in that region is brown, though green elsewhere on the back.

The pigment is always present, whether on the papillæ or between in minute square, pentagonal, and hexagonal patches. The darkness of the skin is probably mainly due to the number of these patches present in any given area.

The antennæ are always green, the brown being almost entirely absent from them, and they are the first to acquire the green colour in the embryo. In fact the young at birth are almost quite white excepting the antennæ.

The colour seems hardly at all affected by the action of spirit. The flesh-coloured brown of the ventral surface is sometimes slightly reddened when the animal is first put into spirit, but the red tinge soon vanishes, being apparently dissolved out by the spirit, which in such cases becomes slightly coloured.

**Ridges and Papillæ of the Skin.**—The skin is thrown into a number of transverse ridges, along which the primary wart-like papillæ are placed.

The papillæ, which are found everywhere, are especially developed on the dorsal surface, less so on the ventral. The papillæ round the lips differ from the remaining papillæ of the ventral surface in containing a green pigment. Each papilla bears at its extremity a well-marked spine.

The ridges of the skin are not continued across the dorsal middle line, being interrupted by the whitish line already mentioned. Those which lie in the same transverse line as the legs are not continued on to the latter, but stop at the junction of the latter with the body. All the others pass round to the ventral surface and are continued across the middle line; they do not, however, become continuous with the ridges of the other side, but passing between them gradually thin off and vanish. The ridges on the legs are directed transversely to the long axes of the legs, *i. e.* are at right angles to the ridges of the rest of the body.

The papillæ of the dorsal surface are not arranged in a single row in the ridges, but in more than one row, in fact a ridge varies in thickness in different parts of its course.

Further, the dorsal ridges are interrupted by thin and sharp, less coloured lines, which are somewhat diagonally arranged, and divide the ridges into lozenge-shaped areas (vide figs. 1 and 10).

**The antennæ** are ringed and taper slightly till near their termination, where they present a slight enlargement.

The rings consist essentially of a number of coalesced primary papillæ, and are, therefore, beset by a number of spines like those of the primary papillæ. They are more deeply pigmented than the rest of the antenna.

The free end of the antenna is covered by a cap of tissue like that of the rings. It is followed by four or more rings placed close together on the terminal enlargement. There appears to be about thirty rings on the antennæ of all adults of this species. But they are difficult to count, and a number of small rings occur, between them, which are not included in the thirty.

The antennæ are prolongations of the dorso-lateral parts of the anterior end of the body.

**The eyes** are paired and are situated at the roots of the antennæ on the dorso-lateral parts of the head. Each is placed on the side of a protuberance which is continued as the antenna, and each presents the appearance of a small crystalline ball inserted on the skin in this region.

The rings of papillæ on that part of the head from which the antennæ arise lose their transverse arrangement. They are arranged nearly concentrically to the antennal rings, and have a straight course forwards between the antennæ.

**The oral papillæ** are placed at the sides of the head. They are attached ventro-laterally on each side of the lips. The duct of the slime gland opens through their free end. They possess two main rings of projecting tissue, which are especially pigmented on the dorsal side; and their extremities are covered by papillæ irregularly arranged (vide description of oral papilla of New Zealand species, p. 175).

**The Buccal Cavity.**—The buccal cavity has the form of a fairly deep pit, of a longitudinal oval form, placed on the ventral surface of the head, and surrounded by a tumid lip.

The lip is covered by a soft skin, in which are numerous

organs of touch, similar to those in other parts of the skin, having their projecting portions enclosed in delicate spines formed by the cuticle. The skin of the lips is raised into a series of papilliform ridges, whose general form is shown in fig. 5; of these there is one unpaired and median behind, and a pair, differing somewhat in character from the remainder, in front, and there are, in addition, seven on each side. The cutaneous papillæ round the front of the lips are raised up and appear like a second outer lip concentric with the anterior part of the real lip, with the posterior part of which it is continuous.

The structures within the buccal cavity are shown as they appear in the surface views in fig. 5. In the median line of the buccal cavity in front is placed a thick muscular protuberance, which may perhaps conveniently be called the tongue, though attached to the dorsal instead of the ventral wall of the mouth. It has the form of an elongated ridge, which ends rather abruptly behind, becoming continuous with the dorsal wall of the pharynx. Its projecting edge is armed by a series of small teeth, which are thickenings of the chitinous covering prolonged from the surface of the body over the buccal cavity. Where the ridge becomes flatter behind, the row of teeth divides into two, with a shallow groove between them.

**The Jaws.**—On each side of the tongue are placed the jaws, which are a pair of appendages, modified in the characteristic arthropodan manner, to subserve mastication. They are essentially short papillæ, moved by an elaborate and powerful system of muscles, and armed at their free extremities by a pair of cutting blades or claws. The latter structures are, in all essential points, similar to the claws borne by the feet, and, like these, are formed as thickenings of the cuticle. They have, therefore, essentially the characters of the claws and jaws of the Arthropoda, and are wholly dissimilar to the setæ of Chætopoda. They are sickle-shaped, and, as shown in fig. 5, have their convex edge directed nearly straight forwards, and their concave or cutting edge pointed backwards. The inner cutting plate has five to eight teeth (fig. 27). The outer plate



has one main tooth (fig. 28), at the base of which is a small tooth. This accessory tooth is found on the outer blade in all South African species. Posteriorly, the behaviour of the two blades is very different. The epithelial ridge bearing the outer blade is continued back for a short distance behind the blade, but the cuticle covering it becomes very thin, and it forms a simple epithelial ridge placed parallel to the inner blade. The cuticle covering the epithelial ridge of the inner blade is, on the contrary, prolonged behind the blade itself as a thick rod, which, penetrating backwards along a deep pocket of the buccal epithelium, behind the main part of the buccal cavity for the whole length of the pharynx, forms a very powerful lever, on which a great part of the muscles connected with the jaws find their insertion.

**The Ambulatory Appendages.**—The claw-bearing legs are in seventeen pairs, and with the exception of the fourth and fifth pairs in both sexes, and the last in the male, they all resemble each other fairly closely. A typical appendage will be first described and the small variations found in the appendages just mentioned will then be pointed out. Each consists of two main divisions, a large proximal portion the leg, and a narrow dorsal, claw-bearing portion, the foot.

The **leg** (fig. 2) has the form of a truncated cone, the broad end of which is attached to the ventro-lateral body wall, of which it appears to be, and is, a prolongation. It is marked by a number of rings of primary papillæ, placed transversely to the long axis of the leg, the dorsal of which contain a green and the ventral a brown pigment. These rings of papillæ at the attachment of the leg, gradually change their direction and merge into the body rings. At the narrow end of the cone there are three ventrally placed pads, in which the brown pigment is dark, and which are covered by a number of spines precisely resembling the spines of the primary papillæ. These spinous pads are continued dorsally, each into a ring of papillæ.

The papillæ of the ventral row next the proximal of these spinous pads are intermediate in character between the primary



papillæ and the spinous pads. Each of these papillæ is larger than a normal papilla, and bears several spines (fig. 2). This character of the papillæ of this row is even more marked in some of the anterior legs than in the one figured; it seems probable that the pads have been formed by the coalescence of several rows of papillæ on the ventral surface of the legs. On the outer and inner sides of these pads the spines are absent, and secondary papillæ only are present.

In the centre of the basal part of the ventral surface of the foot there is present a group of larger papillæ, which are of a slightly paler colour than the others. They are arranged so as to form a groove, directed transversely to the long axis of the body, and separated at its internal extremity by a median papilla from a deep pit which is placed at the point of junction of the body and leg. The whole structure has the appearance, when viewed with the naked eye, of a transverse slit placed at the base of the leg. The segmental organs open by the deep pit placed at the internal end of this structure. The exact arrangement of the papillæ round the outer part of the slit does not appear to be constant.

The **foot** is attached to the distal end of the leg. It is slightly narrower at its attached extremity than at its free end, which bears the two claws. The integument of the foot is covered with secondary papillæ, but spines and primary papillæ are absent, except at the points now to be described.

On each side of the middle ventral line of the proximal end of the foot is placed an elliptical elevation of the integument covered with spines. Attached to the proximal and outer end of this is a primary papilla. At the distal end of the ventral side of the foot on each side of the middle line is a group of inconspicuous pale elevations, bearing spines.

On the front side of the distal end of the foot, close to the socket in which the claws are placed, are two primary papillæ, one dorsal and the other ventral.

On the posterior side of the foot the dorsal of these only is present. The claws are sickle-shaped, and placed on papillæ on the terminal portion of the foot. The part of the

foot on which they are placed is especially retractile, and is generally found more or less telescoped into the proximal part (as in the figure).

The fourth and fifth pairs of legs exactly resemble the others, except in the fact that the proximal pad is broken up into three, a small central and two larger lateral. The enlarged segmental organs of these legs open on the small central division.

The last (17th) leg of the male (fig. 4) is characterised by possessing a well-marked white papilla on the ventral surface. This papilla, which presents a slit-like opening at its apex, is placed on the second row of papillæ, counting from the innermost pad, and slightly posterior to the axial line of the leg.

**The anal papillæ**, or as they should be called, generative papillæ, are placed one on each side of the generative aperture.

**The generative aperture** is subterminal and on the ventral surface. It is inconspicuous in most specimens.

**Internal Anatomy.**—The points of internal anatomy which require to be noted in an account of the species relate entirely to the generative organs. In the male the ductus ejaculatorius (posterior unpaired part of vas deferens, penis of Moseley) is short, and the crural glands of the seventeenth pair of legs are much elongated, reaching forward for a considerable distance in the lateral compartment of the body cavity.

In the female the ovaries are closely approximated and short. They are united to the floor of the pericardium by a single ligament passing off from their front end. Receptacula seminis are absent. The ova contain but little food-yolk. They are oval in shape, and the greatest length of an unsegmented ovum which has passed into the oviduct is .56 to .6 mm.

**Habits.**—They live beneath the bark and in the crevices of rotten stumps of trees, and beneath stones. So far they have only been found, so far as I can ascertain, in the woods on the slope of Table Mountain. They require a moist atmo-

sphere, and are exceedingly susceptible to drought. They avoid light, and are therefore rarely seen, and it is owing to this fact that, though fairly numerous, they were for so long unknown to the inhabitants of the Cape Peninsula. They move with great deliberation, picking their course by means of their antennæ and eyes. It is by the former that they acquire a knowledge of the ground over which they are travelling, and by the latter that they avoid the light. The antennæ are extraordinarily sensitive, and so delicate indeed, that they seem to be able to perceive the nature of objects without actual contact. When irritated they eject with considerable force the contents of their slime reservoirs. The force is supplied by the sudden contraction of the muscular body wall. They can squirt the slime to the distance of almost a foot. The slime, which appears to be perfectly harmless, is extremely sticky, but it easily comes away from the skin of the animal itself.

I have never seen them use their apparatus for the capture of prey. So far as I can judge it is used as a defensive weapon; but this of course will not exclude its offensive use. They will turn their heads to any part of the body which is being irritated and violently discharge their slime at the offending object. Locomotion is effected entirely by means of the legs, with the body fully extended.

Of their food in the natural state we know nothing; but it is probably mainly, if not entirely, animal. Those which I kept in cavity eagerly devoured the entrails of their fellows, and the developing young from the uterus. They also like raw sheep's liver. They move their mouths in a suctorial manner, tearing the food with their jaws. They have the power of extruding their jaws from the mouth, and of working them alternately backwards or forwards. This is readily observed in individuals immersed in water.

The young are born in April and May. They are almost colourless at birth, excepting the antennæ, which are green, and their length is 10 to 15 mm. A large female will produce thirty to forty young in one year. The period of gestation is

thirteen months, that is to say, the ova pass into the oviducts about one month before the young of the preceding year are born. They are born one by one, and it takes some time for a female to get rid of her whole stock of embryos; in fact, the embryos in any given female differ slightly in age, those next the oviduct being a little older (a few hours) than those next the vagina.

The mother does not appear to pay any special attention to her young, which wander away and get their own food.

There does not appear to be any true copulation. The male deposits small, white, oval spermatophores, which consist of small bundles of spermatozoa cemented together by some glutinous substance, indiscriminately on any part of the body of the female. Such spermatophores are found on the bodies of both males and females from July to January, but they appear to be most numerous in our autumn.

The testes are active from June to the following March. From March to June the vesiculæ of the male are empty.

### **Peripatus Balfouri** (n. sp.).

*South African Peripatus, with eighteen<sup>1</sup> pairs of claw-bearing ambulatory legs, of which the last pair is rudimentary; with white papillæ on the dorsal surface.*

*Peripatus Balfouri* resembles very closely *P. capensis*. The points of difference are as follows:

The dorsal skin has an olive-green tinge. The largest papillæ are white, except at their free extremities, which are green (fig. 10). The white spreads out a little round the base of the papillæ. Brown tints are entirely absent in all the specimens which I have examined except one.

The ventral surface is whiter than in *Capensis*, but the papillæ are faintly green. The same remark applies to the ventral surface of the legs.

**The Ambulatory Appendages.**—The claw-bearing legs are eighteen pairs. The legs of the eighteenth pair are smaller

<sup>1</sup> Peters (No. 25) states that there are in the Berlin Museum specimens from the Cape with eighteen pairs of legs (see p. 171).



than the rest (fig. 24). The remaining ambulatory appendages resemble, except in the following points, those of *Capensis*. The three spinous pads are green, and the middle one is broader than the other two; the ventral surface of the proximal part of the leg is white, and the papillæ are a bluish green; the groove at the base is less marked than in *Capensis*.

The foot is rather more delicate than in *Capensis*, and the spines on the ventral side of the base of the claws are placed on two pairs of small papillæ (fig. 9).

The male is distinguished from the female, as in *Capensis*, by the possession of a white papilla on the ventral side of the legs of the seventeenth pair, in the same position as in *Capensis*, and the legs of the eighteenth pair are smaller than in the female. So small are they, indeed, that they are hardly distinguishable from the large papillæ found near the hind end of the body; but they bear two claws, and a rudiment of the foot may be made out.

In the female the legs of the eighteenth pair (fig. 24) present the following features:—The foot seems to be normal and unreduced, but the leg is much reduced, presenting on the ventral side only three rows of papillæ and one spinous pad, which indeed shows, in some specimens more than others, its constitution of separate papillæ. The pad and papillæ are all tinged with green.

The embryos are much smaller than in *Capensis*. In preserved specimens the length of the fertilised ovum is .4 to .48 mm.; and a full sized adult specimen may reach the length of 43 mm. The generative orifice is between the rudimentary legs of the eighteenth pair. As a peculiarity in habits may be mentioned the fact that the individuals of this species nearly always coil themselves into a spiral when touched, while *Capensis* simply contracts and shortens itself.

Locality—Table Mountain.

### Other South African species.

In addition to these two South African species from Table Mountain, the following varieties, some of which at least are probably distinct species, are known.

1. One with fourteen pairs of legs, already named **P. brevis** (Blainville). This species was found by M. Goudot beneath a stone in the woods on Table Mountain. It has been shortly described by Blainville in a note on p. 38 of Gervais' "Études pour servir à l'histoire naturelle des Myriapodes" ('Ann. d. Sci. Nat.,' series ii, vol. vii) as follows:—"Corps subfusiform pourvu de quatorze paires de pattes, noir velouté en dessus, blanchâtre en dessous; longueur totale en comprenant les antennes, 43 mill.; plus grande largeur, 4 mill."

2. Another with nineteen pairs of legs,<sup>1</sup> reported by Mr. Roland Trimen from Plettenberg Bay, Cape Colony, but hitherto undescribed.

3. A third, in my possession, from Table Mountain with twenty pairs of claw-bearing legs, I have found one specimen only. Peters (No. 25) records the existence of specimens from the Cape with twenty pairs of legs (see below p. 171).

4. A fourth, with twenty-one<sup>1</sup> pairs of legs from near Williamstown, South Africa, I have only seen three specimens. They are in the possession of the Indian Museum.

5. A fifth, with twenty-two<sup>2</sup> pairs of legs, of which two specimens are known to me. One of these is in the possession of the Indian Museum; the locality is marked "near Williamstown, S. Africa." The other was found by Mr. J. P. Mansel Weale, and given by him to Mr. Wood Mason, who in his turn gave it to Professor Balfour. This specimen, of which I have not been able to ascertain the exact locality, is in my possession, and is figured on Pl. XVII fig. 8.

<sup>1</sup> There are specimens in the Berlin Museum with nineteen pairs of legs (Peters, No. 25).

<sup>2</sup> Peters (No. 25) records the existence of specimens from the Cape with twenty-one and twenty-two pairs of legs (see below, p. 171).

Of these five varieties I have not seen the first two. I have, however, had full opportunity of examining preserved specimens of the last three and will now shortly describe my observations on them.

**Peripatus with twenty pairs of claw-bearing legs.**—One specimen only—a female—is known to me. Locality, Table Mountain. Length of spirit specimen 23 mm.

The specimen very closely resembles *P. Balfouri*, and would be mistaken for the latter were not its legs counted. The skin presents an identical appearance. The last pair of legs are very small and rudimentary, and the generative opening, which is subterminal just in front of the anus, is between them.

The first nineteen pairs of legs are all normal and resemble exactly, so far as I can judge, those of *P. Balfouri*. In the legs of the twentieth pair, while the foot is normal the leg is much reduced in size. It is entirely without the spinous pads, and possesses only three rows of papillæ of which the row next the foot is slightly tinged with green, the other two being white.

The only other difference which I was able to detect between this specimen and *P. Balfouri* consisted in the very small amount of green on the ventral surface, which is almost white.

On the whole I am not inclined to establish at present a distinct species for the reception of this specimen, but would prefer to regard it provisionally as a variety of *P. Balfouri*.

### **Peripatus Moseleyi.**

*South African Peripatus, with twenty-one and twenty-two pairs of legs.*

All the specimens under this head presented the same general appearance (fig. 24). Were it not for the number of legs they would be taken for specimens of *Capensis*. The ventral surface is light brown and the dorsal an olive green, with scattered brown patches. Green is entirely absent from the ventral surface, excepting on the foot and distal pad, and sometimes a very little on the middle pad. On the dorsal surface there is a band on each side at the base of the legs, in

which the brown papillæ are so numerous as to cause the appearance of a brown band. Elsewhere on the dorsal surface the brown papillæ are very sparsely scattered.

They are all reported from a part of South Africa far removed from Table Mountain, the home of *Balfouri* and *Capensis*, viz. near Williamstown (with the possible exception of the one figured, the locality of which I do not know). Unfortunately I have only been able to see preserved specimens, which, on account of the great contraction they had undergone in dying, were not very favorable for observation.<sup>1</sup>

*Specimens of Peripatus Moseleyi with twenty-one pairs of legs.*—Skin as in *Capensis*. Foot and legs as in *Capensis*. At the bases of some of the legs (no constancy in the different specimens), immediately internal to the opening of the segmental organ, a small white patch of a tumid appearance is present. It occupies the same position as the large tumid papillæ on the ventral side of the leg of *Capensis* (see Pl. XVI, fig. 2), and has been noticed by Wood Mason (No. 23). The generative opening is subterminal, and on each side of it there is an inconspicuous anal papilla. The dorsal side of the foot is marked with streaks of green pigment, arranged parallel to its long axis. The streaks are much less distinct on the anterior than on the posterior feet.

Two of the specimens were smaller than the third, from which they differed by possessing a distinct white papilla on the last (twenty-first) leg, exactly resembling in appearance and position the papilla on the last leg of *Capensis*. I opened one of these smaller specimens, and found it to be a male; while the larger specimen turned out to be a female.

The female was about 26 mm. in length, the male about 20 mm.

*The specimens of P. Moseleyi with twenty-two pairs of legs* were both females. They resemble the specimens with twenty-one legs, so far as I could see from a study of the contracted

<sup>1</sup> Drowning (twenty-four hours or more) and then spirit is the best method of killing *Peripatus* for museum purposes and observation of external characters.



specimens at my disposal, except in two points: (1) in the absence of the anal papillæ, and (2) in the fact that the streaks on the dorsal side of the feet were entirely absent in the first nine pairs of legs. The legs of the last pair resemble, in all respects, the preceding, and the genital opening is behind them.

One of these specimens measured 26 mm. and the other 30 mm. in length.

Inasmuch as I have not been able to find any marked characters associated with the character afforded by the number of legs, and further, as I have had no opportunity of ascertaining whether the latter character is transmitted in reproduction, I am inclined not to establish two distinct species but to regard the specimens with twenty-two legs to be a variety of the species *Peripatus Moseleyi*, which is distinguished by the possession of twenty-one pairs of legs, and a subterminal genital opening behind the last legs.

Peters (No. 25) in a short paper on the variation of the number of legs in *P. capensis*, states that the following specimens were brought to him from Cape Town by a friend of his: three specimens with 22 pairs of legs, eight with 21, eight with 20, one with 19, one with 18, and two with 17 pairs. He adds that they were all found in the same locality, which, however, is not mentioned. He gives no description of the specimens, beyond mentioning the number of legs, and it is not therefore possible to say whether he is right or not in his view that they all belong to the species *Capensis*. I may add that, though I have examined more than a thousand specimens from the Cape Peninsula, I have only seen one specimen with more than eighteen pairs of legs, and not one with less than seventeen pairs.

## CHAPTER III.

### THE AUSTRALASIAN SPECIES—GENERAL CHARACTERS.

*Peripatus* with fifteen pairs of claw-bearing ambulatory legs, with three spinous pads on the legs, and a primary papilla projecting from the median dorsal portion of the foot (figs. 21, 21*a*). The ventral organs are conspicuous, and the males are considerably smaller than the females. The generative opening is between the legs of the last pair, and there are no anal papillæ. The number of legs are constant in all specimens. The ovaries are attached by their whole length to the floor of the pericardium, and each oviduct is provided with a receptaculum seminis. The unpaired portion of the vas deferens is long and complicated in structure. The ova are large and heavily charged with food yolk. The portion of the proximal pad of the fourth and fifth legs which carries the opening of the nephridium is continuous distally with the rest of the pad (fig. 21). A median dorsal white line is present.

Two species are known from the Australasian region; *P. novæ-zealandiæ* from New Zealand, and *P. Leuckarti* from Queensland in Australia.

The former was first described by Captain Hutton (No. 19), the latter by Saenger (No. 15).

### ***Peripatus Novæ-Zealandiæ.***

(Figs. 7 and 17.)

*Australasian Peripatus, without a small tooth at the base of the main tooth of the outer blade of the jaw, and without a white papilla on the ventral side of the last leg of the male.*

The males are considerably smaller and less numerous than

the females. The length of a large female is 50 mm. (2 inches), that of a large male 25 to 30 mm. in the extended condition after drowning. There is no external difference which enables us to distinguish the sexes. The ventral organs, owing to the character of their pigment, are much more conspicuous than in the South African species.

**Colour.**—The colour varies in different individuals (*cf.* figs. 7 and 17). The ground colour varies exceedingly in tint; it consists of a bluish grey, or slate colour, or violet; it is darker on the antennæ than elsewhere, and is especially concentrated in small, dark, square, pentagonal, and hexagonal patches lying close together over the whole surface of the body. Sometimes the outline of these patches is darker than the centre.

The pigment of the papillæ is also much darkened, but this requires a separate description as the variations in the colour of different individuals is mainly due to the papillæ. In all specimens a certain number of the papillæ have brown or orange pigment, which spreads out for a short distance around the base of the papilla, as in the case of the white papillæ of the South African *Peripatus Balfouri*, so that if many of these papillæ occur close together the ground colour is brown or orange and the slate entirely displaced; if such are numerous, they impart a distinctly brown aspect to the specimen. They are scattered irregularly over the whole surface of the body, but are most numerous, as in *Capensis*, in two bands on the sides of the dorsal surface at the base of the legs, where, indeed, in some specimens they almost completely replace the blue.

In most specimens, however, the greater number of papillæ presents a pigment which resembles more or less closely that of the ground colour. In many specimens—perhaps the majority—the papillæ have a dark slate colour; but in some specimens they may have a distinctly blue pigment, and occasionally even a dark purple. The lips, as in *Capensis*, are always destitute of pigment, and, as in that species, there is a sharp line extending along the middle of the whole length of the dorsal surface,

in which the pigment is either absent or of an extremely light shade. On each side of this line the pigment in the papillæ is much darkened. The pads of the legs vary much in colour. In most specimens the distal one is blue, the middle one brown or orange, and the proximal one brown or orange in the centre, and blue along the outer and inner border. In some specimens, however, they are all blue, and in others all brown or orange. In short, it may be said that the colour of the pad varies from blue with hardly any admixture of brown, to brown or orange without any blue. The distal pad is always the most blue. The row of composite large papillæ next to the proximal pad presents the predominant colour of the proximal pad. The blue colour is always absent from the ventral organs, which are either white, brown, or orange.

In all specimens there is a band of especially dark papillæ extending from the ventral extremity of the leg towards the ventral organ (fig. 19). The opening of the segmental organ is placed in the outer end of this band. The ventral surface is almost always mottled, the blue and yellow pigment being distributed in patches; the colour in each kind of patch extending between the papillæ as well as on to them.

**The ridges and papillæ of the skin** are arranged as in the South African species.

**The antennæ** resemble those of the South African species. They are ringed and slightly swollen near the free end (fig. 16). In none of the specimens that I examined did they present any brown pigment. They are entirely of the blue (violet?) grey colour, which forms the ground colour of the skin. The rings are beset with spines, and are covered by closely approximated patches of dark pigment such as have been already described. On the anterior edge of the rings at the front end of the antennæ there is a row of hexagonal, lighter-coloured spaces. At the bases of the spines also the pigment is lighter than elsewhere on the rings. Between the rings spines and patches are absent, and the pigment is of a lighter colour. The free end of the antenna is rounded and covered by a cap of integument resembling that on the rings



and bearing a large number of spines, as in all the species of *Peripatus* that I have seen.

**The eyes** resemble in position and character (fig. 18) those of the South African species.

**The oral papillæ** resemble essentially those of *Capensis*. Fig. 20 shows very clearly the peculiar collapsable joints which this appendage possesses in all the species.

**The buccal cavity, tongue, and lips** resemble in all respects the same structures in the South African species.

**The jaws** differ from those of the latter only in being without the small tooth on the outer blade.

**The ambulatory appendages** (fig. 21) are in fifteen pairs in all the specimens which I have examined. They resemble in their general features the same structures in *Capensis*, so that in the following short description stress will be laid only on the points in which they differ from the latter.

The opening of the segmental organ at the base of the leg is much more indistinct than in *Capensis*, and the peculiar tumid papillæ, which in *Capensis* extends from its outer border on to the ventral surface of the leg, are absent in this species. There are three pads, but the large papillæ of the row adjoining the proximal pad are larger with regard to the ordinary papillæ than in *Capensis*. Sometimes, indeed, they are so large as to present the appearance, unless closely examined, of one continuous spinous pad.

The foot differs from that of *Capensis* in the following points. The two prominent papillæ, placed one on each side (anterior and posterior) of the base of the foot are absent. The dorsal side of the foot near the free extremity possesses a papilla (fig. 21*a*), while the anterior face bears, like the posterior, only one papilla. As in *Capensis*, the opening of the nephridia of the fourth and fifth legs are placed on a small portion of the proximal pad. The part of the pad around the opening is only partly separated from the rest (vide fig. 21). The last leg, so far as I could ascertain, differs only in size (being slightly smaller) from

the preceding, and is without the white papilla found on the last leg of the male of the South African species. Anal papillæ are never present.

**Internal Anatomy.**—As already explained, I do not propose to give in this monograph any detailed account of internal structure. It will be sufficient for my purpose to sum up briefly the more striking differences between the various species.

The internal structure of *Peripatus novæ-zealandiæ* closely resembles that of the South African species. The differences, so far as I have been able to observe them, chiefly concern the generative organs, and the crural glands. It has recently been shown by Miss Sheldon (No. 40) that the crural glands are entirely absent from this species in both sexes.

The generative organs of the male differ from those of the Cape species in three points, viz. : (1) In the much greater length of the terminal unpaired portion of the vas deferens ; (2) in the absence of any specially enlarged crural glands in the last pair of legs ; (3) in the fact (recently shown by Miss Sheldon, No. 40), that the accessory glands, which are longer than in the male of *Capensis*, do not open with the vas deferens, but on the sides of the body outside the nerve-cord and close to the hind end. The terminal unpaired portion of the vas deferens is continuous with the two vasa deferentia (one of which passes as in *Capensis* beneath the two nerve-cords) at the level of the last pair of legs. Thence it is continued forwards for a considerable distance (as far as the level of the eighth legs in some cases) ; eventually bending round to pass backwards to its opening between the last pair of legs. Its walls increase in thickness from before backwards, and are of a distinctly gelatinous consistency in the greater part of their course.

The generative organs of the female differ from those of *Capensis* in two main points, viz. : (1) The two ovarian tubes are much longer, extending from the level of the eleventh to that of the thirteenth, and sometimes to that of the fourteenth pair of legs, and are entirely separate from one another, each being suspended throughout its entire course to the pericardial

floor by a distinct membrane. (2) There are two spherical receptacula seminis, each of which opens into the oviduct by two ducts; and the oviduct in the neighbourhood of these openings is slightly sacculated.

It will be remembered that in the Cape species the ovarian tubes were closely applied together and united to the pericardial floor only at their anterior extremities by a single band.

Spermatozoa have been found in the receptaculum and in the oviduct near the opening of the latter. There are few, if any, spermatozoa in the ovary. I have not been able to see, though I have examined live specimens with great care, a trace of cilia in any part of the female organs. It will be seen from the above that I take exception to Captain Hutton's<sup>1</sup> description of the ovary as an ovate organ.

The ova are large, oval in shape, and heavily charged with food-yolk. They are surrounded by a membrane of the same nature as the egg membrane of *P. capensis*, but much tougher. The greatest length of an unsegmented ovum from the uterus is about 1.5 mm., the breadth .8 mm. The greatest number of embryos found in one animal was eighteen, twelve in one uterus and six in the other. But the number varies in the different specimens. Captain Hutton found eighteen in one uterus and eight in the other. The same naturalist states that "when the embryos are numerous there is a considerable difference in the point of development to which they have attained." I can confirm this statement; but the greater number of the embryos in any given animal are of the same age.

**Habits.**—Captain Hutton (No. 19) has fully described the habits of this species. He says:

"They live in decayed wood, under stones, or in crevices of rock. They are nocturnal, but will feed in the daytime when hungry. They feed upon animals. I have seen one shoot out its viscid fluid from the oral papillæ at a fly introduced into the jar in which it was confined, and stick it down;

<sup>1</sup> I have not been able to see any trace of the lateral vessel of Captain Hutton.



it then went up and sucked its juices, rejecting the whole of the integument. This viscid fluid is for offensive and not defensive purposes. In the winter they become half torpid, though procreation still goes on. During this time of the year I have never seen them feed, and they cannot emit their viscid fluid, or only in very small quantity. They move with deliberation, entirely by means of their legs, the body being much lengthened. When walking, the antennæ are constantly moved about as feelers. If a needle is placed upright immediately in front of one, the antenna is drawn past it without actual contact; but the points of the hair probably touch the needle. Although viviparous, the eggs are often extruded before the development is complete, but these always die."

From the study of the living specimens brought by Mr. Evans I have been able to confirm Captain Hutton's observation as to the habits of the species, so far as it was possible to do so on imported specimens.

I have not been so fortunate as to see them catching flies with their slime, but this is not to be wondered at considering the greatly changed conditions in which I observed them. In fact I have failed to keep the specimens alive for any length of time in this country.

Having received two lots, one in July and the other in December, I am able to make some conjectures as to the period of gestation. Captain Hutton asserts that they breed all the year round. The only other statement concerning the breeding is, so far as I know, by Moseley (No. 20). He states that the young are born in July. This is undoubtedly correct, for the live specimens received by me at the end of July gave birth to fully-developed young on the voyage, and directly after reaching England, and those examined contained, in the great majority of cases, either old embryos or none at all.

On the other hand, the specimens which came in December contained, in the great majority of cases, unsegmented and segmenting ova. But in a few (small specimens) the uterus was empty, and again, in a still smaller number, there were old embryos, and in some a few old embryos coexisted with the



more numerous young ova. These observations seem to me to show that the eggs pass into the uterus in November and December, and that the young are born in July; in other words, that the period of gestation is eight or nine months. This conclusion is, however, not borne out by Captain Hutton's statement<sup>1</sup> (No. 19), that he has "never opened one which did not contain embryos;" and that he found the uterus full of embryos in September and November. It must be admitted, therefore, that the point cannot be settled on the evidence before us. It is much to be regretted that none of the New Zealand naturalists have taken the trouble to determine a point so easy of observation.

With regard to the sexual relations, I am inclined to think that copulation does not take place, and that the end of the vas deferens, which I have called the ductus ejaculatorius, is not protrusible. I have, indeed, observed in spirit specimens small white ovoid bodies, which closely resemble the spermatophores of the South African species, and I think there can be no doubt that the sexual relations are the same as in those species. The period of the year at which fertilisation is effected is unknown. Hutton has observed that the receptacula contain spermatozoa in November, but are empty in September. This observation distinctly confirms my deduction that the ova pass into the oviduct in November or December.

Before leaving this subject I may mention that I can entirely confirm Hutton's statement that the eggs are often extruded before the development is completed. This may possibly be a reminiscence of the time, probably not very remote, when the eggs were laid in the normal Arthropodan manner—a view which receives support from the thick shell, large size, and heavily yolked nature of the ovum of this species.

<sup>1</sup> It should be noted that Hutton does not state whether his observations were spread over the whole year.

**Peripatus Leuckarti.**

Locality, Queensland.

*Australasian Peripatus, with fifteen pairs of legs, an accessory tooth on the outer blade of the jaw, and a white papilla on the ventral side of the last leg of the male.*

The following observations were made on two specimens most kindly placed at my disposal by Professor Jeffrey Bell, to whom they were sent by Dr. Ramsay, of Sydney. They were found (vide No. 44) near Wide Bay in Queensland. The finder's name has not been communicated to me. (See postscript A.)

Both the specimens were much contracted and the feet bent ventrally on the legs, so that it was difficult to get a good view of the ventral surfaces of the feet.

The length of large specimen	.	.	.	16—17 mm.
„ „ small „	.	.	.	9—10 mm.

The large specimen was a female, and the small a male.

Generally it may be said of these specimens that they resemble almost exactly the New Zealand species. After careful search I have only been able to find three minute points of real difference between them. These are:

1. The outer blades of the jaws have an accessory tooth at the base of the main tooth, as in the Cape species.

2. The male has a rounded white papilla on the ventral face of the fifteenth leg, on each side of the genital opening. It is in the same position with regard to the leg as the corresponding structure in the Cape males.

3. The pigment on the ventral surface is much less conspicuous in this than in the New Zealand species, so that the mottled appearance presented by the ventral surface of the latter species is not found in these specimens. The pigment on the ventral surface of these specimens is much more marked in the lower parts of the papillæ than elsewhere. In the skin between the papillæ and at the apices of the papillæ the pigment is so faint as to be hardly discernible. The result

is that to the naked eye the ventral surface appears quite pale with coloured papillæ projecting from it. The predominant pigment of the ventral surface is the blue, but orange is present. The hind end of the ventral surface in the region of the last three legs is darker than elsewhere, in consequence of the great number of the pigmented papillæ.

In addition to the above characters, it may be mentioned that the genital papilla of the female is remarkably prominent, and bears at its free end a longitudinally disposed slit. In the male the genital papilla is fairly prominent, but its aperture is wider and more rounded, resembling the same structure in both sexes of the New Zealand species. I append a short general description of the two specimens.

There are fifteen pairs of legs. The ventral surface is pale, dotted uniformly with pigmented papillæ, which are more numerous behind. The dorsal surface is dark, and has a median white line. The pigment is of the two colours found in the New Zealand species, viz. bluish to green, and orange to brown. The blue pigment is much the most conspicuous on the dorsal surface. The antennæ are blue mainly, but possess some orange pigment arranged in rings round their basal halves.

The genital papilla, which is remarkably prominent in the female, is between the legs of the fifteenth pair. The feet and legs resemble exactly, so far as could be made out, those of the New Zealand species. The feet have the median dorsal papilla so characteristic of that species; there are three pads on the legs, and a patch of blue pigment round the opening of the nephridia.

If there is any difference, it relates to a faint double row of somewhat turgid papillæ proceeding outwards from the opening of the nephridium along the ventral surface of the leg. The same feature is present in a much more marked form in *P. capensis*. The opening of the nephridium is perhaps slightly more conspicuous than in the New Zealand species. The last leg of the male presents a white papilla on its ventral surface. The outer blade of the jaw has an accessory tooth.

The internal anatomy resembles, so far as I could make out, that of the New Zealand species.

In the female the ovaries were attached along their whole length, and possessed numerous oval white eggs of an average length of .27 mm. In addition there were some larger eggs of a yellowish colour, some of which were attached to the ovary, and some broken away and lying in the body cavity. The largest of these measured .75 mm. in length. They were full of yolk and without any visible membrane.

Each oviduct possessed the receptaculum seminis in a position similar to that of the same structure in *Peripatus novæ-zealandiæ*. The uterus was empty.

In the male the genital organs were normal, and the unpaired portion of the vas deferens was long, and apparently of a similar structure to that of the New Zealand species.

The specimens were not sufficiently well preserved for an examination for the accessory glands.



## CHAPTER IV.

### PERIPATUS FROM THE NEOTROPICAL REGION.

*Peripatus* is found all over the northern part of the Neotropical region. It is reported from Chili, Columbia, Cayenne, Venezuela, Nicaragua, and from many of the West Indian Islands, viz. Jamaica, Cuba, Trinidad, St. Thomas. I unfortunately have only been able to make a complete study of the species from Venezuela and of that from Demerara; of some of the remainder I have only seen single specimens, or specimens the preservation of which was not sufficiently good to allow of the determination of specific characters. A partial exception must be made in favour of the small species from Trinidad, of which Dr. J. v. Kennel has been good enough to send me two specimens; but these were, unfortunately, somewhat contracted and not sufficient in number to enable me to generalise as to specific characters. I trust, however, that the careful description of the Venezuela species, the specimens of which were collected by Professor Ernst at Caracas, and given to Professor Balfour, will form a groundwork on which future collectors of *Peripatus* from this region will be able to work.

Although I have failed in determining the relations between the various specimens of *Peripatus* which have been found in the Neotropical region, still I have seen enough to be able to establish a certain number of characters which distinguish a great number—and probably all—of the neotropical *Peripatus* from those found in other regions. Those characters are stated in the following definition :

### General Characters of the Neotropical Species.

With four spinous pads on the legs, and two papillæ on the anterior side of the foot. With generative aperture between the legs of the penultimate pair. Dorsal white line absent, and papillæ arranged in a single row on the ridges of the skin. Many of the primary papillæ have a terminal portion slightly constricted off from the main portion. Outer blade of jaw with one minor tooth, inner blade with one minor tooth next the main tooth (fig. 25), and a row of smaller minor teeth separated from the latter by a diastema. Unpaired part of vas deferens of great length. Ovary with oviducts entering its anterior end, and attached to pericardial floor by a single band of great length from the opposite end. Each oviduct provided with a receptaculum seminis with double duct, and with a thin-walled receptaculum ovorum. Ova minute without yolk. Embryos of very different ages in same uterus, and births probably taking place all the year round. Males generally smaller than females, and frequently with a smaller number of legs. The number of legs often inconstant in the same species in the same sex; in fact it may be said that the number of legs varies in all the Neotropical species which are at all well known. The opening of the nephridium of the fourth and fifth legs is on a papilla which is quite separate from the third pad (fig. 11).

### *Peripatus Edwardsii.*

*Neotropical Peripatus from Caracas with a variable number of legs—the smallest number being twenty-nine pairs and the greatest thirty-four. Males with twenty-nine and thirty pairs of legs, and tubercles on a varying number of the posterior legs. The basal parts of primary papillæ are cylindrical.*

I propose to reserve the name *Edwardsii* for the Neotropical species, which is best known, viz. that from Caracas. This has been described by Ernst (No. 26) and Gaffron (No. 35). Whether the specimens obtained by Audouin and Milne-Edwards from Cayenne and named *Edwardsii* by Blanchard

(No. 8) belong to this species cannot be definitely settled until more specimens come to hand.

In **P. Edwardsii** the females are larger than the males and have a greater number of legs. This fact was first noticed by Gaffron. He found that the males possessed either twenty-nine or thirty pairs of legs, while of his females one had thirty-four, four had thirty-two, and four thirty-one. In my specimens, which came, I believe, from the same place as the specimens which Gaffron used for his<sup>1</sup> second paper (No. 35), all the males had thirty or twenty-nine pairs of legs (four with thirty and three with twenty-nine), while of the females three had thirty-one, four had thirty-two, and one thirty-three (fig. 6). Ernst states that the full-grown animal has thirty-one pairs of legs, the new-born young but twenty-nine; and he deduces from this that the young are born with an incomplete complement of legs, and that new legs make their appearance in the subsequent growth of the animal. This, if true, would be important, as in no species of *Peripatus* that I know of are the young born imperfect in this respect. I therefore examined the number of legs of the oldest embryos in my specimens with great care, and the result of my observations is in entire contradiction to Ernst's statements. The embryos I found differ in the number of legs, just as do the adults, the greatest number being thirty-two pairs and the smallest twenty-nine. If this is so there can be no doubt that the new-born young differ in the same manner. To take an instance: from the lower end of the uterus of the four specimens with thirty-two pairs of legs I obtained in all seven embryos, which were practically fully-developed and ready for birth. Of these, four had twenty-nine pairs, two had thirty-one, and one had thirty-two—an embryo with twenty-nine and one with thirty pairs were found in the same mother; and I have also found instances of a quite immature embryo (but possessed of the full number of legs) with a greater number of legs than the large mature embryo which occupied the part of the uterus

<sup>1</sup> The specimen which Gaffron used for his first paper was from Trinidad, and had thirty-two pairs of legs.

next the external opening. Considering the easy nature of the observations required, Professor Ernst's statements display a very extraordinary method of work.

**Colour.**—My observations on this point were made on spirit specimens, and cannot therefore have the value of those of Ernst, who had the living animals before him. He says: "The colour is brownish black, with a diffused black line on the middle of the back; the ventral side is dark flesh-coloured."

In all my preserved specimens the colour was brown, darker in some than in others; in the specimen figured it is as dark as in any in my possession. The ventral surface, moreover, was of the same colour as the dorsal. As these specimens came from Caracas, and have become distinctly paler since I first saw them, it seems pretty clear that the colour of this species is much affected by spirit. It will be remembered the brown pigment of *P. capensis* was changed by the action of spirit. The same fact has been observed by Grube (see below, p. 480), who found that the pigment was partly dissolved by the spirit, and also by myself in some specimens brought alive from Demerara by Mr. W. L. Sclater (No. 41).

**The Ridges and Papillæ of the Skin.**—The ridges are more clearly marked, and the papillæ of the dorsal surface are less numerous. The dorsal white line is not present, so that the ridges are continuous right across the dorsal middle line. Further, there is for the most part only one row of papillæ on each ridge, whereas in the South African and New Zealand species there is considerable irregularity in this respect. The fine diagonal lines, which break up the rows of papillæ into lozenge-shaped areas, are absent in this species. The ridges extend for the most part right across the dorsal surface, but here and there, particularly at the level of the legs, there are accessory ridges extending across the middle line and stopping short a little distance on each side of it. They cause a slight deflection of the contiguous main ridges (fig. 6). Many of the papillæ—particularly those on the legs—are divided by a constriction into two main portions (fig. 12)—



a free portion bearing the spine and a larger basal part. The basal part is cylindrical, and the terminal portion often of considerable size. Those immediately round the lips appear to be without this characteristic.

**The antennæ** present no features of specific interest. The tongue and lips are without pigment and have the typical form.

**The jaws** present differential characters. The outer blade (fig. 26) has a well-marked minor tooth in addition to the main one. On the inner blade the number of minor teeth varies (generally eight), and the anterior of them is close to the main tooth and larger than the rest, which are separated from it by a diastema (fig. 25).

**The oral papillæ** are normal.

A typical **ambulatory appendage** presents the following characters (fig. 12). The leg possesses four spinous pads, a strongly marked, rather deep groove in the position of the tumid papillæ of *Capensis*, i.e. a groove placed on the ventral surface of the leg, and extends from the opening of the nephridium as far as the third or fourth row of papillæ from the proximal pad. This groove may be widely open as in the leg figured, or its edges may be approximated so that it appears as a slit. The papillæ at its margin are somewhat larger and more indistinct than the ordinary papillæ. The foot resembles that of *Capensis* in possessing two papillæ on its anterior face, but the two basal papillæ are absent.

The opening of the segmental organ of the fourth and fifth legs is on a papilla which is placed on the proximal side of, and quite separate from, the third pad, between it and the proximal pad (fig. 11). This feature is found in all the neotropical species which I have examined. On certain of the posterior legs of the males there are two and sometimes one smooth white tubercle with an opening at their extremities (fig. 22). They are placed close behind the groove, and are found only on the posterior legs. Their exact arrangement varies in different individuals. To give examples :

In a male with 30 pairs of legs :

*Right side.*—Legs 21—24 inclusive, each had one such tubercle ; legs 25—28 inclusive, each had two such tubercles ; legs 29 and 30 were without them.

*Left side.*—Leg 21 had one tubercle ; leg 22 was without one ; legs 23 and 24 each had one ; legs 25—28 inclusive, each had two ; legs 29 and 30 were without them.

In another male with 30 pairs of legs :

*Right side.*—Leg 23 had one tubercle ; legs 24—28 inclusive, each had two ; legs 29 and 30 were without.

*Left side.*—Leg 22 had one ; legs 23—28 inclusive, each had two ; legs 29 and 30 were without them.

When one papilla only is present it is the distal one.

From these examples it is obvious that the arrangement of these tubercles is different not only in the different individuals but also on opposite sides of the same individual. The legs of the last two pairs are always without them. Gaffron found precisely the same irregularity in the arrangement, but in his specimens they were symmetrical. In one with thirty pairs of legs, the legs of the 22nd pair each had one, and those of the 23rd to the 28th pair each had two tubercles. While in another male with twenty-nine pairs, the legs of the 20th pair had only one each, while the legs of the 21st to the 27th pair each had two. The pits at the apices of these tubercles are, according to Gaffron, the openings of glands corresponding to the crural glands of *Capensis*.

The legs of the last pair are smaller than the penultimate, and possess only two spinous pads. The legs of the penultimate pair are without the nephridial opening, and the pedal groove is inconspicuous as it is in the last pair. I could not satisfy myself whether the legs of the last pair possessed a nephridial opening ; but Gaffron states that they possess a nephridium.

Gaffron (No. 35) describes a peculiar bean-shaped papilla, placed in a pit of the integument on the dorsal surface of the leg near the foot. Its surface is smooth, as is also the lining of the pit in which it is placed. It is found in the Trinidad species, and may very probably turn out to be characteristic of the neotropical species.

**Internal Anatomy.**—Excepting the generative organs there is nothing in the internal anatomy of this species which deserves notice here. The generative organs, of which we have an excellent description by Gaffron, do, however, present some features of interest. The generative opening in both sexes is between the legs of the penultimate pair. The oviduct end of the ovary is directed forwards, and the ovarian ligament, which is attached to the opposite end of the ovary, is of great length, being attached to the pericardial floor between the twenty-fifth and twenty-sixth pairs of legs. A globular receptaculum seminis (with two short ducts) opens into the anterior part of each oviduct. Immediately in front of the receptacula each oviduct gives off a short diverticulum, called “cæcum” by Ernst, “zipfelformige Anhang,” and “ovarial-trichter” by Gaffron. Gaffron, who at first thought that this process opened at its free end into the body cavity, now accepts Kennel’s statement that it opens into a small vesicle with extremely thin walls. Kennel calls this vesicle the receptaculum ovarum. I have seen the process, but, unfortunately, have no observations on its termination; but I am strongly inclined, on theoretical grounds, to think that Kennel is correct in his statement as to the delicate vesicle. The generative ducts are the modified nephridia of the segment on which the external opening is placed: this is proved, on the one hand by their development, and on the other by the fact that nephridia are absent from the penultimate legs, between which the generative opening is placed. Now, it has been shown by me (No. 39) that all the nephridia open internally, not into the body cavity as has been supposed, but into a small vesicle with extremely delicate and thin walls. It thus appears that the presence of this delicate vesicle of the receptaculum ovarum is another proof—if another were wanted—that the oviducts of *Peripatus* are modified nephridia. No such structure has been found in the New Zealand species, but, possibly, further investigations may come upon it. In *Capensis*, for reasons which I have set forth elsewhere (No. 39), one would not expect to find this structure.



The male organs differ from those of the Cape species and resemble those of the New Zealand species in the fact that the common posterior part of the testicular ducts is of great length. A very good description of it has been given by Gaffron. A pair of accessory glands is present in the male. They open on each side of the anus (Gaffron).

Nephridia are present in the legs of the last pair but are absent from the penultimate legs, between which the generative opening is placed (Gaffron, No. 35). With regard to the **crural glands**, Gaffron states that they are absent from the female, and only present in the males in those legs provided with the tubercles described above.

The ova are small and without yolk. Their development has been described in a closely-allied species from Trinidad by Kennel, according to whom the embryos acquire a placental connection to the uterine wall and an amnion. These structures are, however, said to disappear after a certain stage is reached, and there is reason to doubt whether they have the relations, significance, and method of development which Kennel ascribes to them (Sclater, No. 46).

The uterus contains embryos in all stages of development, and the young, which are fully developed at birth, are presumably born at different times of the year.

The length of mature embryos of *Peripatus Edwardsii*, lying stretched out in the uterus with head near generative opening, is about 20 mm.

The length of a large adult female is 55 to 60 mm. The males, of course, are rather smaller.

**Habits.**—The habits of this species are apparently much the same as in the other species. A large number of specimens were found by Ernst in a yard of the University building of Caracas under heaps of rubbish.

Peters (No. 24) mentions specimens from the following localities in Venezuela:—Caracas, Puerto Cabello, Laguayra. He states that some of the specimens from Puerto Cabello have thirty and others thirty-two pairs of legs.



### **Peripatus from Demerara.**

IN January of this year (1887) Mr. W. L. Sclater brought to England twenty female specimens of *Peripatus* collected at Maccasseema, on the Pomeroon River. The specimens, when they came into my hands, were torpid and apparently at the point of death, and it was necessary to open them at once and remove the embryos. I was unable therefore to make a detailed examination of them in the fresh state.

Mr. Sclater has already (No. 41) given a short description of the specimens. To his description I add here notes of my own observations, made on the first arrival of the animals, and an account of those which I have since made on their preserved bodies.

All the specimens (twenty in number) were females. The colour was a dark brown on the dorsal surface, with a median diffuse dark stripe, such as Ernst describes. The antennæ were of a darker colour than the rest of the body. The ventral surface was of a lighter colour than the dorsal—a kind of flesh colour. The animals turned quite red in spirit, and the red colouring matter was gradually dissolved by the spirit leaving them a lighter brown.

In well-grown specimens the uterus contained ten embryos in each horn, of which the fifth from the ovary was generally in the spiral stage. The receptacula ovarum seemed to contain ova, which were .038 mm. in diameter. The large eggs in the ovary were the same size.

In one specimen, which I carefully examined for the purpose, there were cilia in the receptacula seminis in the position described by Gaffron. There can be no doubt of their presence. I saw them in active movement. I am very glad to have had the chance of confirming Gaffron on this point. The older embryos had the same colour as the adult. I could not be certain of the presence of spermatozoa in either the receptaculum seminis or in the oviduct. If present at all, they must have been few in number,

To these observations I have now the following to add: The colour, under the prolonged action of spirit, has become lighter. The antennæ, oral papillæ, jaws and legs, resemble in all respects the same structures in the Caracas specimens. The grooves on the legs were for the most part closed and therefore slit-like. None of them possessed tubercles.

Mr. Sclater has the following statement on the slits and tubercles. "In my specimens and in that from Dominica, the openings (i. e. the slits) are in many cases rounded, and sometimes have attached to them a bladder-shaped appendage." I do not quite understand this passage, but if it means that the slits are round openings and that there are tubercles in the specimens he brought from Demerara, I cannot confirm his statement. It is unfortunate that no males are to hand, as it is important from a systematic point of view to know if they have the tubercles such as are found in the Caracas species, and if they differ from the females in the number of legs. The length of a large specimen was 55 to 60 mm.

Mr. Sclater states that all the specimens examined by him, including those taken from the uterus, had thirty pairs of legs. Mr. Sclater's observations must have been confined to a very small number of his specimens. I examined fourteen adults: of these seven had thirty pairs of ambulatory legs, six had thirty-one, and one had twenty-seven. Out of thirteen embryos examined seven have thirty pairs and six have thirty-one. Unfortunately, I did not notice that the adults varied in the number of their legs, until after the embryos had been removed from all except the specimens with twenty-seven pairs of legs; so that it was not possible to determine, excepting in this case, whether the young resembled their parents in this respect. Out of four embryos which had already developed the full complement of legs and were removed from the specimen with twenty-seven pairs, three had twenty-seven and one had twenty-eight pairs of ambulatory legs, so that it appears that the number of legs varies in the species.

The only other difference between these specimens and those from Caracas that I could detect, related to the primary

papillæ on the skin. In the Caracas species, as already mentioned, these have comparatively narrow cylindrical bases, and the diameter of the tops is often almost as great as that of the basal portion. In the Demeraran specimens, on the other hand, the lower portion of the papillæ have the form of truncated cones with very broad bases, while the tops are relatively, and I think absolutely, much slenderer than in the Caracas specimens. The papillæ figured by Gaffron (No. 34, Pl. VII, and here reproduced fig. 29) resemble those of the Demeraran specimens, and will serve for comparison with the papillæ of the Caracas specimens shown on Pl. XVIII, fig. 12. I propose provisionally to regard these specimens as belonging to a distinct species, and to call it **P. demeraranus**<sup>1</sup> with the following characters. *Neotropical Peripatus with twenty-seven to thirty-one pairs of ambulatory legs and cylindrical primary papillæ. Locality Maccasseema, Demerara.*

### **Peripatus from Trinidad.**

Dr. J. v. Kennel (No. 31) found two distinct species of *Peripatus* in Trinidad; one of these he calls *P. Edwardsii* and the other *P. torquatus*. His description of both is unfortunately extremely meagre.

The species which he calls *Edwardsii* possesses twenty-eight to thirty pairs of legs (No. 32). The generative opening is between the legs of the penultimate pair, and the generative organs present the characters of the Neotropical species.

Dr. Kennel was kind enough to send me two of this species in spirit, and I am able to supplement his description.

<sup>1</sup> Sclater (No. 46) gives the name *im Thurni* to the specimens with thirty pairs of legs, which he has observed. It is of course quite possible that the specimens with thirty pairs may be specifically distinct from those with twenty-seven and thirty-one pairs. This, however, as stated above, I do not regard as probable. On account of this uncertainty, and also because of the further uncertainty as to whether the Demeraran specimens are specifically distinct from species already determined and named, I propose the provisional name of *Demeraranus* to include all specimens from Demerara, whether the number of legs be twenty-seven, thirty, or thirty-one pairs.



One of these specimens had thirty-one pairs of legs and the other thirty, from which it appears that Kennel, like so many other zoologists who have examined *Peripatus*, has not been very careful in counting the legs. The dorsal surface was of a chocolate colour, the ventral surface being a light brown. The papillæ and ridges of the skin presented the features characteristic of the Neotropical species. The bases of the primary papillæ are conical as in *Demeraranus*. The jaws also presented no points of difference from those of the species from Caracas, excepting that possibly the number of minor teeth was rather larger: in one I found as many as eleven.

I think there can be no doubt that this is a distinct species, and I propose to call it and define it as follows:

***Peripatus Trinidadensis* (*Edwardsii*, Kennel).**

*Peripatus* from Trinidad, with twenty-eight to thirty-one pairs of ambulatory legs, and a large number of minor teeth on the inner blade of the jaw. The basal portions of the primary papillæ are conical.

***Peripatus torquatus* (Kennel).**

*Peripatus* from Trinidad of large size, with forty-one to forty-two pairs of ambulatory legs. The head is marked off from the body by a bright yellow band on the dorsal surface.

The larger species is named *P. torquatus*, and Kennel gives the following description of it. "The females reach the length of 15 cm., with a diameter of 8 mm., while the males have a length of about 10 cm. The colour of the dorsal surface is red brown, the middle line of the back being somewhat darker, and paling off towards the sides. The head with the tentacles is black and is marked off from the body on the dorsal side by a bright yellow band, which often shows a small interruption in the middle line. The ventral surface has a dark flesh colour. There are forty-one or forty-two pairs of legs.

This completes the list of the Neotropical *Peripatus* of which we have anything like detailed knowledge. The remain-



der of this monograph will be devoted to a statement of all that is known with regard to the specimens found in other localities.

1. The original species found by Guilding (No. 1) in the forests of the Island of St. Vincent in the Antilles, and called by him *P. juliformis*, possessed thirty-three pairs of legs, and a dark line down the centre of the back. The generative opening is apparently immediately in front of the penultimate legs. The animal was of a fair size, being three inches in length by three lines in breadth. It is apparently similar in all essential respects to other neotropical *Peripatus*, and I am inclined to maintain for the present the species, and to define it as follows :

***Peripatus juliformis* (Guilding).**

*Neotropical Peripatus from St. Vincent, with thirty-three pairs of ambulatory legs.*—This definition is exceedingly unsatisfactory because it is based on the number of legs, which, as I have stated, varies in all the species which have been closely examined.

2. The species described by Audouin and Milne-Edwards (No. 2) possessed thirty pairs of ambulatory legs, and came from Cayenne (on the banks of the River Approuague, three leagues from its mouth). The specimens were found “unter faulem, im Schlamme versunkenem Holze, an den Ufern des Approuage im Brackwasser.”

The description is very imperfect, as may be judged from the fact that the generative aperture is not even mentioned.

The species was regarded by the authors as identical with Guilding's *P. juliformis*, but subsequently Blanchard (No. 8) gave it the name of *P. Edwardsii*. I propose to retain the latter name and to regard it as belonging to the same species which I have fully described above from Caracas.

It must, however, be remembered that the characters of *P. Edwardsii*, as given in this monograph (p. 184) are based on the Caracas specimens ; and it may quite well happen that the

*Peripatus* found at Cayenne, when better known, will turn out to be a distinct species.

3. Wiegmann (No. 4) obtained a specimen of *Peripatus* from near the Valentia Lake in Columbia, with thirty pairs of legs. It is quite impossible to say whether this is a distinct species or not. It possesses, according to Wiegmann's description, four spinous pads on its legs and a generative opening between the legs of the penultimate pair.

4. C. Mority (No. 5) obtained a large number of *Peripatus* from the Island of St. Thomas. He gives no details.

There is a specimen in the British Museum from St. Thomas. It has twenty-eight pairs of ambulatory legs, and is of a yellowish-brown colour, but is unfortunately too ill-preserved for determining any specific characters.

5. Peters (No. 24) mentions specimens from Utuado, Porto Rico, and gives the following particulars.

Specimens	21 mm. in length	had	27	pairs of legs.
„	33 mm.	„	30	„
„	38 mm.	„	31	„
„	42—48 mm.	„	32	„

6. Blanchard (No. 8) has described a *Peripatus* found in Chili by M. Claude Gay, with nineteen pairs of legs. His description is as follows:—"Le corps est long de 30 à 32 mill., et large de 5 à 6, légèrement atténué aux deux extrémités, mais surtout vers la partie postérieure. Sa couleur est noire, un peu variée irrégulièrement de taches roussâtres. La tête est presque carrée avec les antennes amincies vers le bout, présentant des annulations très serrées. L'orifice buccal est ovalaire. Les pattes sont au nombre de dix-neuf paires, ciliées de poils raides comme de petites pointes, et terminées par des crochets."

There is obviously nothing in this description which enables us to say whether the three specimens at the author's disposal possessed the characters of the Neotropical species or not. It is extremely probable, considering the remoteness of the locality, that this is a distinct species; but unfortunately

Blanchard has not, with the exception of a name, assigned to it any feature which can be in the least degree regarded as specifically distinctive. He calls it *P. Blainvillei*, and says that it has nineteen pairs of legs. The name I propose to discard, and the statement of fact I am inclined to doubt, for this reason:—In Gay's 'Historia de Chile,' vol. iii, "Zoologia," p. 58, there is a description of this proposed new species, and the possession of nineteen pairs of legs is given as a character. I presume Blanchard is responsible for this statement as it coincides with that given in No. 8. In the description reference is made to some figures in the Atlas. These turn out to be a dorsal, ventral, and side view, &c., of the specimen described. Will it be believed that not only does each of these figures show a different number of legs, but in the case of the dorsal and ventral views, the numbers on the right and left sides are different? The details are as follows:

Dorsal view, right side,	27	legs and oral papilla.
"    "    left    "	26	"    "
Ventral "    right  "	33	"    "
"    "    left    "	31	"    "
Side view of left side,	20	"    "

I do not know who is responsible for these figures. The draftsman's name on the plate is Spinola. I need hardly say that, if they are a fair sample of the drawings in the Atlas, the zoological plates are not worth the paper they are printed on.

It will, perhaps, be convenient to denote the fact that there is a *Peripatus* in Chili, by introducing for it the provisional name of ***Peripatus chiliensis***.

7. Blanchard refers to a *Peripatus* found in Cuba by M. Macleay. He regards it as belonging to the species *juliformis*. I have been unable to find any account of this Cuban species.

8. Grube (No. 11) describes three specimens of *Peripatus* from near Colonia Towar, in Venezuela, and referred them to *P. Edwardsii*. One of the specimens possessed twenty-nine pairs of legs and the other two thirty each. But one cannot regard his statements on this head as being trustworthy, in-

asmuch as the specimen he has figured has thirty-one pairs (in addition to the oral papillæ).

He found a number of embryos in the uteruses of his specimens, all of which, excepting one with thirty, possessed thirty-one pairs of legs.

His statement on the colour is interesting, as tending to show that the pigment in this species is affected by the prolonged action of spirit. He says :

“Die Färbung war an einem sehr frisch erhaltenen Weingeist exemplar ein dunkles unreines Kirschroth, der Weingeist, indem es lag, hatte sich blassroth gefärbt, bei denen die längere Zeit aufbewahrt waren, ging der Ton in's Braunlichgrue über, doch blieb die Rückenseite immer sehr viel dunkler als die Bauchseite, auch zeigte sie beständig die schon von den früheren Beschreibern erwähnte mittlere Längsfurche von noch dunklerer Farbe, rechts und links von ihr in einiger Entfernung sieht man gewöhnlich noch eine dunkle Seitenlinie.”

I cannot be quite certain from Grube's figures whether the papillæ have the form characteristic of the Caracas species or of the Demerara form.

The species possesses all the Neotropical characters, viz. inner blade of jaw with minor teeth separated by diastema from the first small tooth, legs with four spinous pads, generative opening between the penultimate pair of legs, oviducts with receptaculum and process, embryos in uterus of very various ages.

I propose, therefore, to retain provisionally Grube's name for the specimens from Colonia Towar, and to regard them as belonging to the species found at Caracas, and described above as *P. Edwardsii*.

9. Mr. Thomas Belt found a specimen of *Peripatus* at Santo Domingo, in Nicaragua. The specimen (dried) is referred to in his work, 'The Naturalist in Nicaragua' (p. 140), and has been examined by Professor Moseley, who found that it possessed thirty-one pairs of ambulatory legs.



**P. quitensis** (Schmarda).

10. Professor Jeffrey Bell has recently (No. 43) drawn attention to a reference by Schmarda in his 'Zoology' (No. 42) to a species with thirty-six pairs of legs from Quito, in Ecuador. Schmarda gives a figure of the specimen, which came from an elevation of 9000 feet.

**Neotropical Peripatus in the British Museum.**

1. Specimen from Dominica found by Mr. G. F. Angas. This specimen is in excellent condition, and has twenty-nine pairs of ambulatory legs. It has been shortly described by Professor Jeffrey Bell (No. 29), who says that it has thirty pairs of legs. This may be so, but I could not make out more than twenty-nine. The dorsal surface is brown, and there is a dark streak (chocolate-coloured with a dash of purple) running along the sides of the body just dorsal to the legs. The legs are without tubercles. The pedal grooves are widely open. The papillæ are, I think, conical in form; but the light was not good enough to enable me to obtain certainty on this point.

2. A specimen marked *P. Blainvillei*, without locality. This has thirty-three pairs of ambulatory legs, and is of a reddish-brown colour. It is very much contracted. There were no tubercles, and I was not able to make out the shape of the papillæ.

3. A specimen marked *P. Blainvillei*, without locality (see above, p. 196), with twenty-eight pairs of ambulatory legs.

4. There are three specimens in a bottle labelled "From Jamaica," collected by Gosse.

They are all a yellowish brown. Two of them have thirty-one and one thirty-seven pairs of ambulatory legs. The latter is remarkable as being the smallest of the three, measuring in the contracted condition 22 mm. Of the two with thirty-one pairs of legs, the largest measured about 48 mm., and the other about 22 mm. The papillæ were conical and there were no tubercles. Mr. Gosse, in 'A Naturalist's Sojourn in Jamaica' (P. H. Gosse, London, Longmans,

1851, p. 66), states that these *Peripatus* are found at Bluefields mountain above Bluefields House, near the town of Savanna-le-Mar. The mountain height is four or five miles from Bluefields. Here, around a piece of burnt ground just reclaimed from the forest, but not yet planted, were found, under stones, five or six specimens of *Peripatus*, one twice as large as any of the others. The piece of ground lay at the foot of a conical peak of considerable elevation, but not the very loftiest, covered with original forest. "It is a curious creature, and I think rather allied to the Annelida than the Mollusca. It is of a velvety appearance, of a blackish-brown hue, the tentacles tipped with white. From these latter organs there exudes, when the animal is touched, a thick glutinous substance, as adhesive as birdlime." He concludes that it is of a different species from that found by the Rev. L. Guilding at St. Vincent.

5. A specimen labelled "*Peripatus juliformis*, West Indies, Mr. Gibson, *Nereis viridis*, Adams, 'Linn. Trans.,' feet only thirty-one pairs."

This specimen is about 65 mm. in length,  $5\frac{1}{2}$  in breadth, 5 in dorso-ventral depth; i. e. it is cylindrical in form. It possesses thirty-two pairs of ambulatory legs, and has a very pale brown colour (almost white). Its skin is much smoother than is generally the case.

The legs have four spinous pads, and are without tubercles; the generative opening is between the legs of the penultimate pair; the integumentary papillæ are constricted; the legs of the last two pairs are very small. It clearly, therefore, belongs to a typical Neotropical species, but more than this cannot be said.

6. A smaller specimen with thirty pairs of ambulatory legs of very much the same colour and form. It was labelled, "*Peripatus juliformis*, Guild., W. Indies? Sloane collection."

It possesses thirty pairs of legs. The generative opening is between the legs of the penultimate pair. The grooves on the base of the legs fairly well marked. Feet not sufficiently well preserved for study (claws broken away). The integu-

mentary papillæ constricted, and arranged on the dorsal surface in regular rows. Length about 48 mm.; body cylindrical in shape with a diameter of about 4 mm. The legs are without tubercles.

7. Finally there is a specimen labelled "*Peripatus Santarem*, Wickham, purchased of W. H. J. Carter." It has thirty-one pairs of ambulatory legs, and presents, so far as its external features are concerned, the Neotropical characters. The papillæ are conical, and the legs are without tubercles.

Professor Steenstrup was kind enough to send me for examination the specimens in his museum. I desire to take this opportunity of thanking him for his courtesy and kindness in the matter. The Copenhagen specimens were in four bottles:

(1) Label "*Peripatus Edwardsii*, Bl., Vestindien, Krøyer." This was a fine, well-preserved specimen, with thirty-one pairs of ambulatory legs, and a brown colour. The dorsal surface was darker than the ventral. The dorsal papillæ were remarkably large (fig. 14) and constricted, as were also the ventral, but less markedly. The generative opening was between the legs of the penultimate pair, and the spinous pads of the legs were four in number.

(2) Label "*Peripatus Edwardsii*, Blanch., St. Croix, Krøyer." This specimen, which in general appearance resembled the first, but was smaller, possessed twenty-seven pairs of ambulatory legs. Spinous pads and generative opening as in (1).

(3) Label "*Peripatus Vestindien*, Hombek (?)." With thirty-two pairs of ambulatory legs.

(4) The specimen in the fourth bottle was not sufficiently well preserved for observation.

It is unfortunate that the exact localities of the above were not recorded. They are obviously all Neotropical species, but to which of these they belong cannot be at present settled.

Four specimens of *Peripatus*, of which one had thirty-one pairs of legs, are reported from Demerara (Hoorubea Creek, twenty miles from Georgetown, on east side of Demerara river), by Mr. J. J. Quelch (No. 36). No details are given.

A single specimen was found at Breves, on the Island of Marajo, at the mouth of the Amazon, by Mr. J. C. Branner (No. 37). No details are given.

#### PERIPATUS SUMATRANUS.

A single specimen of *Peripatus*, stated to have come from Sumatra, has recently been described by Dr. R. Horst (No. 38). The evidence that the specimen was actually found in Sumatra is not, however, conclusive. Dr. Horst states that it was found in a bottle containing insects from East Sumatra. The name of the finder is not given, and there is no evidence to show how the specimen got into the bottle. Considering the fact that this is the only specimen of *Peripatus* ever reported from the Oriental region, it will be prudent to suspend our judgment as to the authenticity of the locality given by Dr. Horst. The specimen has twenty-four pairs of ambulatory legs, and is 25 mm. in length. The papillæ are constricted as in the Neotropical species, and are apparently on the cylindrical type. Dr. Horst describes them as "appearing to consist of a truncated cone, bearing on its top a small cylinder provided with a spine." The legs have four pads, the generative opening is between the legs of the penultimate pair. All these are Neotropical characters. The anus is not quite terminal. Colour is dark blackish brown; the ventral surface is paler, greyish. "Some small white spots scattered on the dorsal surface, but they seem only to be produced by the loosening of the cuticle from the top of the papillæ." The foot carries only two papillæ, one on the anterior and one on the posterior face. This is unique so far as my experience of *Peripatus* goes. The pedal groove is absent from the two posterior legs as in *P. Edwardsii*. The antennæ have forty-seven rings.

I think that there can be no doubt that this is a distinct species. It is the only specimen hitherto recorded from the Oriental region, and it seems a fact of extreme interest that it should resemble the Neotropical species more than any other. It is a great misfortune that Dr. Horst was not able to examine the jaws and generative organs.



**Peripatus sumatranus (Horst).**

*Peripatus from Sumatra, with twenty-four pairs of ambulatory legs, four pads on the legs, and constricted papillæ. The generative opening is between the legs of the penultimate pair. The feet have only two papillæ.*

## SYNOPSIS OF THE SPECIES OF PERIPATUS.

**South African Species.**

*With three spinous pads on the legs and two primary papillæ on the anterior side of the foot, and one accessory tooth on the outer blade of the jaw; with a white papilla on the ventral surface of the last fully developed leg of the male. Genital opening subterminal, behind the last pair of fully-developed legs. The terminal unpaired portion of vas deferens short. (Ova of considerable size, but with only a small quantity of food-yolk.)*

- P. capensis** (Grube).—*South African Peripatus, with seventeen pairs of claw-bearing ambulatory legs. Locality, Table Mountain. P. 157.*
- P. Balfouri** (Sedgwick).—*South African Peripatus, with eighteen pairs of claw-bearing ambulatory legs, of which the last pair is rudimentary. With white papillæ on the dorsal surface. Locality, Table Mountain. P. 166.*
- P. brevis** (De Blainville).—*South African Peripatus, with fourteen pairs of ambulatory legs. Locality, Table Mountain. (I have not seen this species. Presumably it has the South African characters.) P. 168.*
- P. Moseleyi** (Wood Mason).—*South African Peripatus, with twenty-one and twenty-two pairs of claw-bearing ambulatory legs. Locality, near Williams-town, Cape Colony. P. 169.*

**DOUBTFUL SPECIES.**

- (1) *South African Peripatus, with twenty pairs of claw-bearing ambulatory legs (Sedgwick). Locality, Table Mountain. (Also Peters, locality not stated.) P. 168.*
- (2) *South African Peripatus, with nineteen pairs of ambulatory legs (Trimen). Locality, Plettenberg Bay, Cape Colony. (Also Peters, locality not stated.) P. 168.*

**Australasian Species.**

*With fifteen pairs of claw-bearing ambulatory legs, with three spinous pads on the legs, and a primary papilla projecting from the median dorsal portion*

of the feet. Genital opening between the legs of the last pair. Receptacula seminis present. Unpaired portion of vas deferens long and complicated. Ova large and heavily charged with yolk.

- P. Novæ-zealandiæ** (Hutton).—*Australasian Peripatus*, without an accessory tooth on the outer blade of the jaw, and without a white papilla on the base of the last leg of the male. New Zealand. P. 172.
- P. Leuckarti** (Saenger).—*Australasian Peripatus*, with an accessory tooth on the outer blade of the jaw, and a white papilla on the base of the last leg of the male. Queensland (N. S. Wales, Victoria, vide postscript A). P. 180.

### Neotropical Species.

*With four spinous pads on the legs, and the generative aperture between the legs of the penultimate pair. Dorsal white line absent. Primary papillæ divided into two portions. Inner blade of jaw with gap between the first minor tooth and the rest. Oviducts provided with receptacula ovorum and seminis. Unpaired part of vas deferens very long and complicated. Ova minute, without food-yolk. (Legs not constant in number in the same species.)*

- P. Edwardsii**.<sup>1</sup>—*Neotropical Peripatus* from Caracas, with a variable number of ambulatory legs (twenty-nine to thirty-four). Males with twenty-nine or thirty legs, and tubercles on a varying number of the posterior legs. The basal part of the primary papilla is cylindrical. P. 184.
- P. Trinidadensis** (n. sp.).—*Neotropical Peripatus* from Trinidad, with twenty-eight to thirty-one pairs of ambulatory legs, and a large number of teeth on the inner blade of the jaw. The basal portion of the primary papillæ is conical. P. 194.
- P. torquatus** (Kennel).—*Neotropical Peripatus* from Trinidad, with forty-one to forty-two pairs of ambulatory legs. With a transversely placed bright yellow band on the dorsal surface behind the head. P. 194.

### DOUBTFUL SPECIES.

The above are probably distinct species. Of the remainder we do not know enough to say whether they are distinct species or not. The following is a list of these doubtful species, with localities and principal characters.

- P. juliformis** (Guilting).—*Neotropical Peripatus* from St. Vincent, with thirty-three pairs of ambulatory legs. P. 195.

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<sup>1</sup> This name was first applied by Blanchard (No. 8) to a species from Cayenne (vide above, p. 195). The description, however, is very imperfect, and it is by no means clear that the Cayenne species is identical with the species here named *Edwardsii*.

- P. Chiliensis.**—*Neotropical Peripatus from Chili, with nineteen pairs of ambulatory legs.* P. 197.
- P. demeraranus.**—*Neotropical Peripatus from Maccasseema, Demerara, with twenty-seven to thirty-one pairs of ambulatory legs and cylindrical primary papillæ.* P. 191.
- Peripatus from Cayenne** (Audouin and Milne-Edwards).—*With thirty pairs of legs.* Named **P. Edwardsii** by Blanchard. P. 195.
- Peripatus from Valentia Lake, Columbia** (Wiegmann).—*With thirty pairs of legs.* P. 196.
- Peripatus from St. Thomas** (Moritz).—No description. P. 196.
- Peripatus from Colonia Towar, Venezuela** (Grube).—*With twenty-nine to thirty-one pairs of ambulatory legs.* Named **P. Edwardsii** by Grube. P. 197.
- Peripatus from Santo Domingo, Nicaragua** (Belt).—*With thirty-one pairs of ambulatory legs.* P. 198.
- Peripatus from Dominica** (Angas).—*Neotropical Peripatus, with twenty-nine pairs of ambulatory legs.* P. 199.
- Peripatus from Jamaica** (Gosse).—*With thirty-one and thirty-seven pairs of ambulatory legs.* P. 198.
- Peripatus from Santarem.**—*Neotropical Peripatus, with thirty-one pairs of ambulatory legs.* P. 201.
- Peripatus from Cuba.**—No details. P. 197.
- Peripatus from Hoorubea Creek, Demerara** (Quelch).—*With thirty pairs of legs.* P. 201.
- Peripatus from Marajo** (Branner).—No details. P. 202.
- Peripatus from Utuado, Porto Rico** (Peters).—*With twenty-seven, thirty, thirty-one, and thirty-two pairs of legs.* P. 196.
- Peripatus from Surinam** (Peters).—No details. No. 24.
- Peripatus from Puerto Cabello, Venezuela** (Peters).—*With thirty and thirty-two pairs of legs.* P. 190.
- Peripatus from Laguayra, Venezuela** (Peters).—No details. P. 190.
- Peripatus Quitensis** (Schmarda).—*From Quito, with thirty-six pairs of legs.* P. 199.
- P. Peruanus** (Grube).—*Vide* postscript B.

### **Peripatus from Sumatra (?).**

- P. Sumatranus** (Horst).—*Peripatus from Sumatra, with twenty-four pairs of ambulatory legs, and four spinous pads on the legs. The primary papillæ of the neotropical character with conical bases. Generative opening between the legs of the penultimate pair. Feet with only two papillæ.* P. 202.

## SUMMARY OF DISTRIBUTION.

## DISTRIBUTION OF THE SOUTH AFRICAN SPECIES—

Slopes of Table Mountain, neighbourhood of Williamstown, Plettenberg Bay—Cape Colony.

## DISTRIBUTION OF THE AUSTRALASIAN SPECIES—

Queensland—Australia.

North and South Islands—New Zealand.

## ORIENTAL REGION—

Sumatra (?).

## DISTRIBUTION OF THE NEOTROPICAL SPECIES—

Nicaragua.

Valencia Lake, Caracas, Puerto Cabello, Laguayra, Colonia Towar—Venezuela.

Quito—Ecuador.

Maccasseema, Hoorubea Creek—Demerara.

Surinam (Peters).

Cayenne.

Santarem, Marajo at the mouth of the Amazon—Brazil.

Chili.

Peru (Grube).

and in the following West Indian Islands—Cuba, Dominica, Porto Rico (Peters), Jamaica, St. Thomas, St. Vincent, Trinidad.

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POSTSCRIPT A.

Since writing the account of the Queensland specimen on pp. 180—182, I have received a letter from Mr. A. Sidney Olliff, of Sidney, and a specimen of *Peripatus*, which he, in conjunction with Mr. H. Merewether, found last year in New South Wales at Cassilis, on the banks of the Mounmoura Creek, a tributary of the Goulbourn River. Mr. Olliff (No. 47) gives the following description of the specimen :—“ It possesses fifteen pairs of claw-bearing leg-appendages and a pair of oral



papillæ . . . . . During life my specimen was coloured as follows: shining slaty-brown above, dusted with brick red, with a dusky-red patch on the head, and a moderately distinct dusky-red lateral line on each side extending throughout its entire length; below, pinkish grey; the antennæ dark brown. It measured 21 mm. when fully extended." Mr. Olliff in the same letter draws my attention to the fact that the specimens of *Peripatus Leuckarti* from Queensland, described on p. 180 et seq., were found by Mr. Tryon, who<sup>1</sup> records it from Brisbane and Cardwell. He further points out to me that Mr. J. J. Fletcher has a note on the "Discovery of *Peripatus* in Victoria" on p. 450 of the 'Proceedings of the Lin. Soc. of New South Wales,' 1887. The Victorian specimen was found by Mr. R. T. Baker at Warragal, Gippsland. It possesses fifteen pairs of claw-bearing legs and a pair of oral papillæ. The Australian localities at present known are therefore Cardwell and Brisbane, in Queensland; Cassilis, in New South Wales; and Warragal, in Victoria.

In addition to calling my attention to these new localities, Mr. Olliff has most kindly sent me his specimen—the only one which at the date of his letter (9th May, 1888) had been found. It appeared to me to resemble the two specimens from Queensland, described above on p. 180; but I must confess that I have not had time or opportunity to make a sufficiently minute examination of it. This I do not regret, as the task will be much better and more completely performed by naturalists on the spot who are able to examine the living specimens.

I may here again call attention to the fact, that by far the best way of killing *Peripatus* for the examination of external features is to drown them thoroughly, i.e. until the muscular tissue is dead and does not contract when the animals are placed in spirit. This generally requires an immersion in the water for twenty-four hours or more. I may also remind collectors of the living animals that they are liable to come out of their box at night or in the dark, if any hole be left for

<sup>1</sup> 'Proceedings of the Linnean Soc. New South Wales,' 1886.

their escape; and that they are able to make their way through astonishingly small apertures.

Lastly, I venture to express a hope that we may not have to wait so long for an account of the development of the Australian *Peripatus* as we have for that of the New Zealand species. In the light of what we know of the development of the other species of this genus, it cannot fail to be a most interesting study in morphology, and one which would well repay investigation. For this purpose the eggs should be taken out of the uterus of the fresh animal, and if they are heavily yolked, as I believe they are, should be preserved in a saturated solution of corrosive sublimate for a few minutes; or, better still, in a mixture of 1-4th per cent. solution of chromic acid and acetic acid, as recommended by Miss Sheldon in her forthcoming second paper on the development of the New Zealand species.

#### POSTSCRIPT B.

Dr. Paul Mayer has kindly pointed out to me that I have overlooked a paper by Grube (No. 48) on *Peripatus peruanus*. The specimen is stated to come from Jelski, in Peru. Grube describes it as being 30·3 mm. in length, and 4·5 mm. in breadth in the middle; as having twenty-nine pairs of feet, of which twenty-eight are provided with claws. Colour dark brown, with black furrow along the middle of the back, which is covered with white warts; on the ventral surface there is a longitudinal row of whitish spots; the genital opening is between the feet of the penultimate pair.

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## EXPLANATION OF PLATES XIV, XV, XVI, XVII, XVIII, XIX, and XX.

### PLATE XIV.

*Peripatus capensis*, drawn from life. Life size. From a drawing by Mr. E. Wilson.

### PLATE XV.

*Peripatus capensis*.  $\times 4$ . Dorsal view of a spirit specimen. From a drawing by Miss Balfour. This figure was originally published in vol. xxiii of this Journal.

### PLATE XVI.

The figures on this Plate originally appeared in vol. xxiii of this Journal. They are from drawings by Miss Balfour.

FIG. 2.—A leg of *P. capensis*, ventral view.  $\times 30$ .

FIG. 3.—A right leg of *P. capensis*, viewed from the front side.

FIG. 4.—The last leg of a male specimen of *P. capensis*, ventral view to show the papilla, at the apex of which the accessory gland of the male, or enlarged crural gland, opens to the exterior.

FIG. 5.—Ventral view of head and oral region of *P. capensis*.

### PLATE XVII.

FIG. 6.—*P. Edwardsii*.  $\times 4$ . Dorsal view of a specimen with thirty-three legs. From a drawing by Miss Balfour.

FIG. 7.—*P. novæ-zealandiæ*.  $\times 4$ . Dorsal view. From a drawing by Miss Balfour.

FIG. 8.—*P. Moseleyi*.  $\times 4$ . Dorsal view. From a drawing by Miss Balfour.

FIG. 9.—Fourth leg of *P. Balfouri*. Ventral view. From a drawing by Mr. E. Wilson.

FIG. 10.—A piece of skin from the dorsal region of *P. Balfouri*. From a drawing by Mr. E. Wilson.

FIG. 11.—Terminal portion of fourth leg of *P. Edwardsii*. From a drawing by Mr. E. Wilson. (The colour of this figure is not that of the specimen.)

## EXPLANATION OF PLATES XVIII, XIX, XX.

### PLATE XVIII.

All the figures on this Plate, except Fig. 16, are from drawings by Mr. Wilson. Fig 16 is from a drawing by Mr. Hill.

FIG. 12.—Leg of *Peripatus Edwardsii*. Ventral view.

FIG. 13.—Head of *P. Edwardsii*. Ventral view.

FIG. 14.—Portion of skin of one of the Copenhagen West Indian specimens, labelled *P. Edwardsii*.

FIG. 15.—Sixth left foot of *P. novæ-zealandiæ*. Front view.

FIG. 16.—Terminal part of antenna of *P. novæ-zealandiæ*.  $\times 120$ .

### PLATE XIX.

All the figures on this Plate, except Figs. 21 and 21*a*, are from drawings by Mr. W. H. Hill, executed under the supervision of Professor Moseley. Figs. 21 and 21*a*, by Mr. Wilson.

FIG. 17.—*P. novæ-zealandiæ*. A specimen of another colour. Dorsal view.  $\times 6$ .

FIG. 18.—Head of *P. novæ-zealandiæ*.  $\times 32$ . Dorsal view.

FIG. 19.—Portion of ventral surface of *P. novæ-zealandiæ*.  $\times 28$ .

FIG. 20.—Oral papilla of *P. novæ-zealandiæ*.  $\times 100$ .

FIG. 21.—Fourth leg of *P. novæ-zealandiæ*. Ventral view.

FIG. 21*a*.—Foot of the same fore-shortened, so as to show the dorso-median papilla.

### PLATE XX.

Figs. 22, 23, 24, 25, 26, from drawings by Mr. Wilson. Figs. 27 and 28, from drawings by Miss Balfour.

FIG. 22.—Ventral view of a posterior leg of *P. Edwardsii*.

FIG. 23.—Ventral view of hind end of *P. novæ-zealandiæ*.

FIG. 24.—Ventral view of hind end of *P. Balfouri*.

FIGS. 25 and 26.—Jaw blades of *P. Edwardsii*.

Fig. 25. Inner blade. The diastema is rather too marked.

Fig. 26. Outer blade.

FIGS. 27 and 28.—Jaw blades of *P. capensis*.

Fig. 27. Inner blade.

Fig. 28. Outer blade.

FIG. 29.—Skin of ventral portion of leg (close to the pads) of *P. Trinidadensis*, copied from Gaffron. The figure shows the form of the simple papillæ, and two of the composite papillæ of the row next the proximal pad.

FIG. 30.—Skin of leg of *P. novæ-zealandiæ*. From a drawing by Mr. Hill.

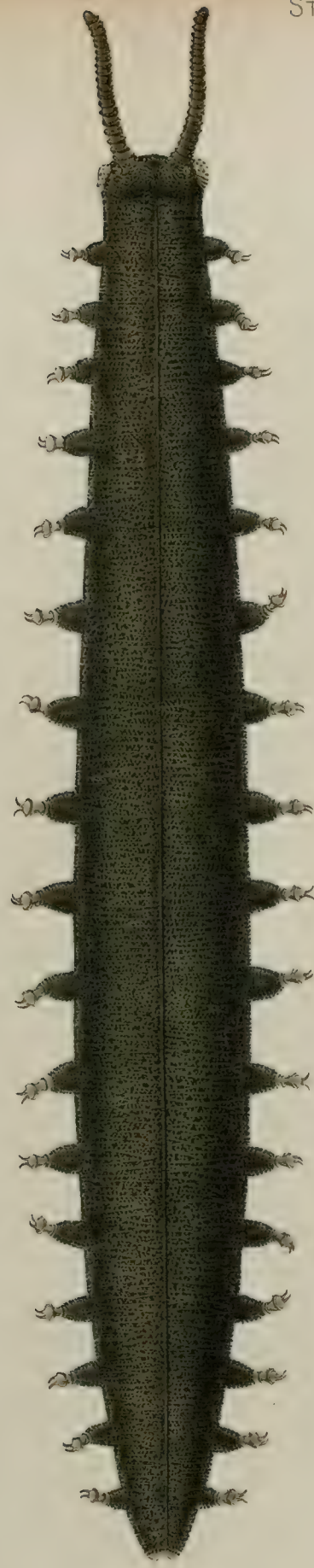




*Peripatus fapensis*. Drawn from life, Life size.



Fig. 1

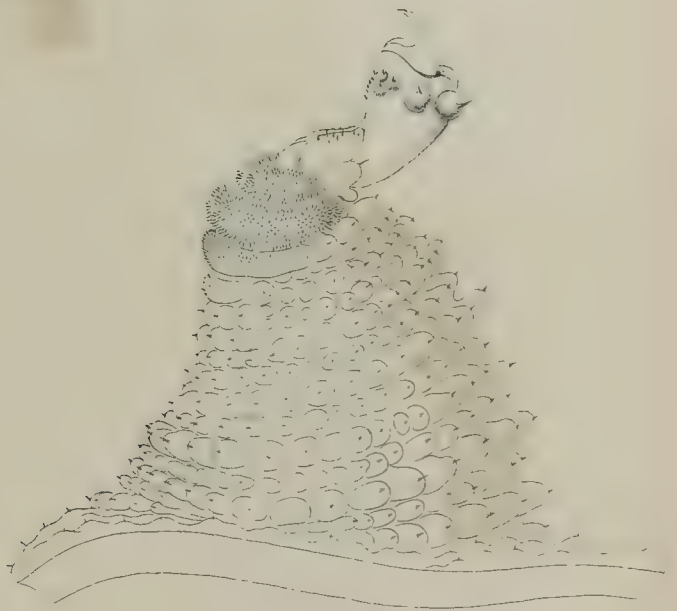








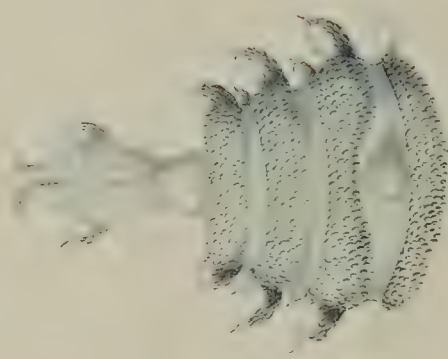
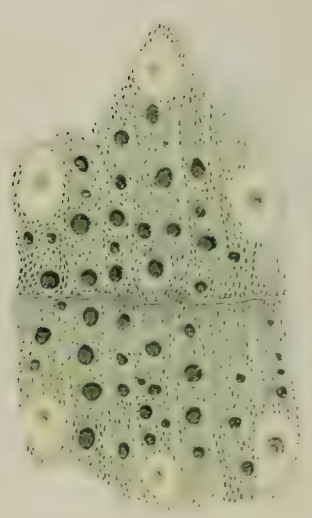
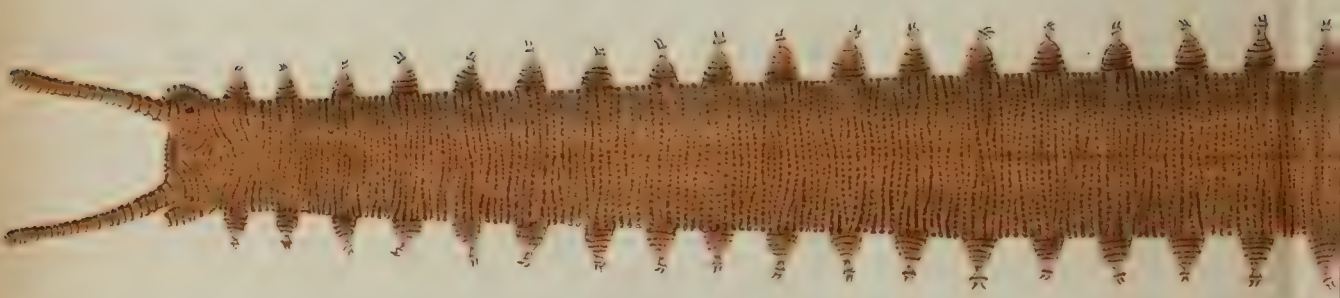












4<sup>th</sup> leg of P. Balfouri.  
Fig 9

4<sup>th</sup> leg of P. Edwardsii



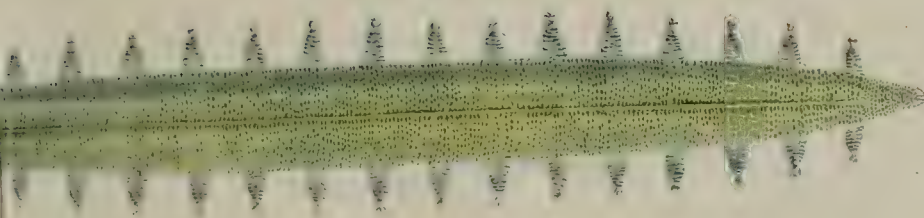
P Moseleyi x 4.

Fig 8



P Edwardsii x 4

Fig 6.



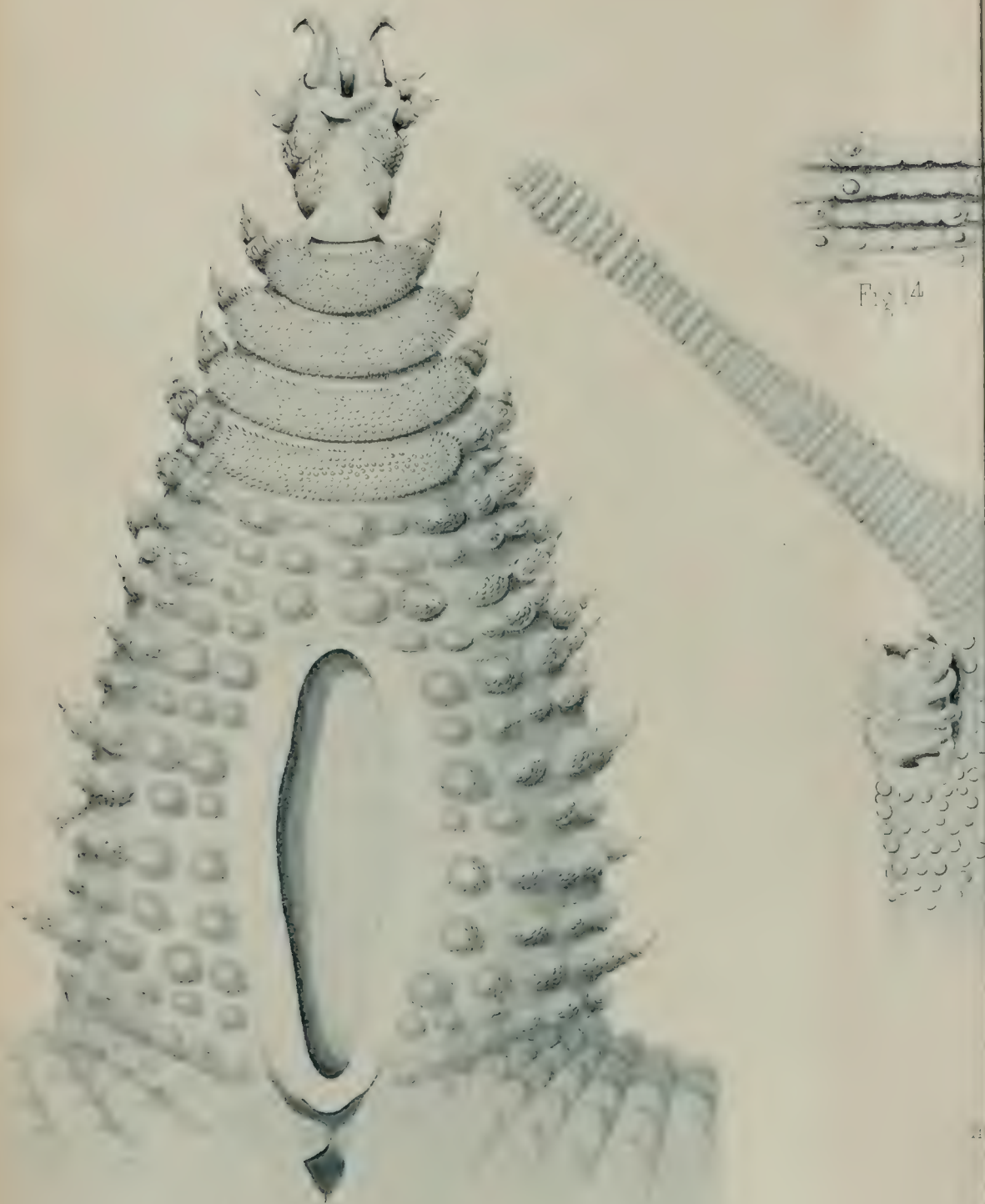
P Novae Zeelandiae x 4.

Fig 7.









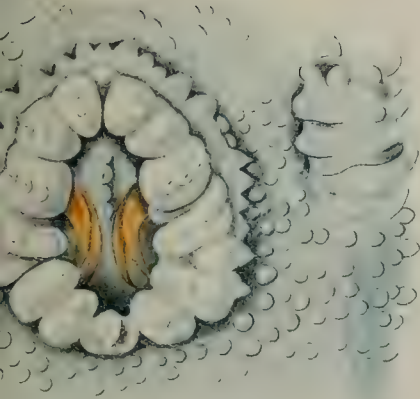
Ventral view of a leg of *T. Edwardsoni*.

Fig 12.

6<sup>th</sup> left foot of *P. Novae Zealandiae* Anterior view



Fig 15



6<sup>th</sup> left foot of *P. Edwardsii* ventral view

Fig 13

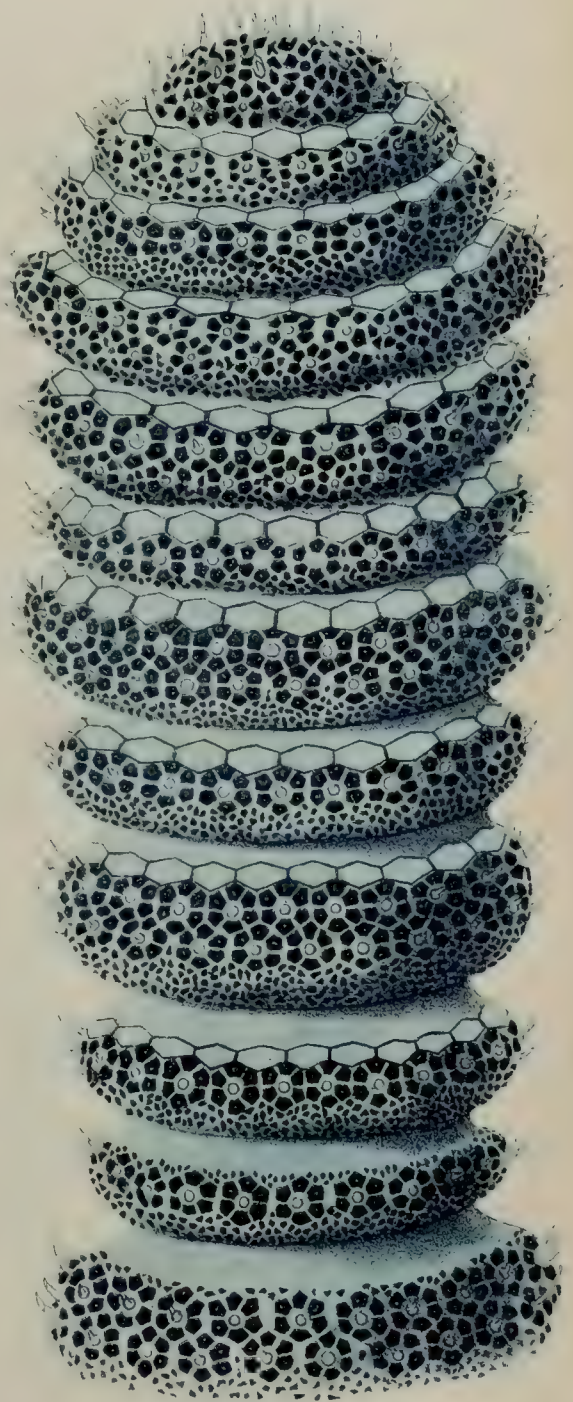


Fig 16







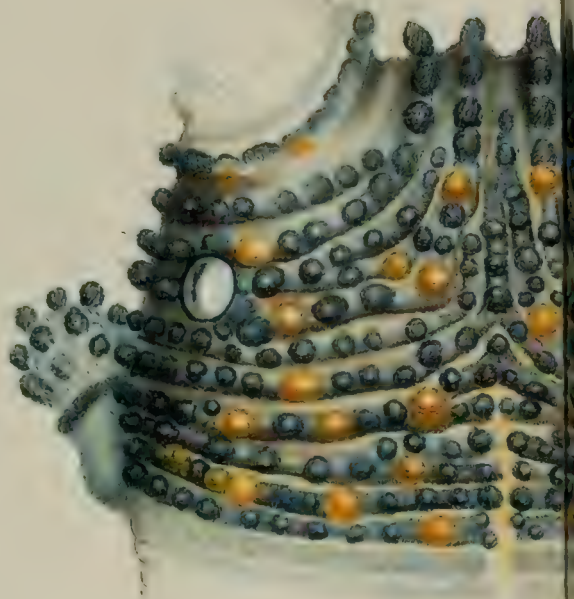
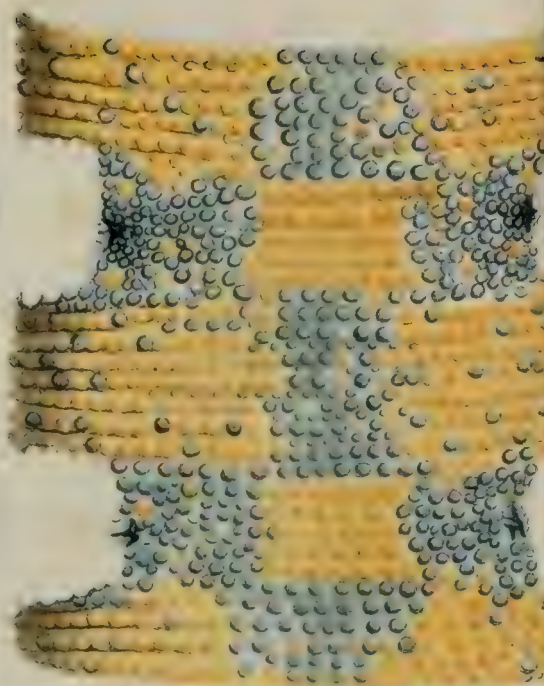
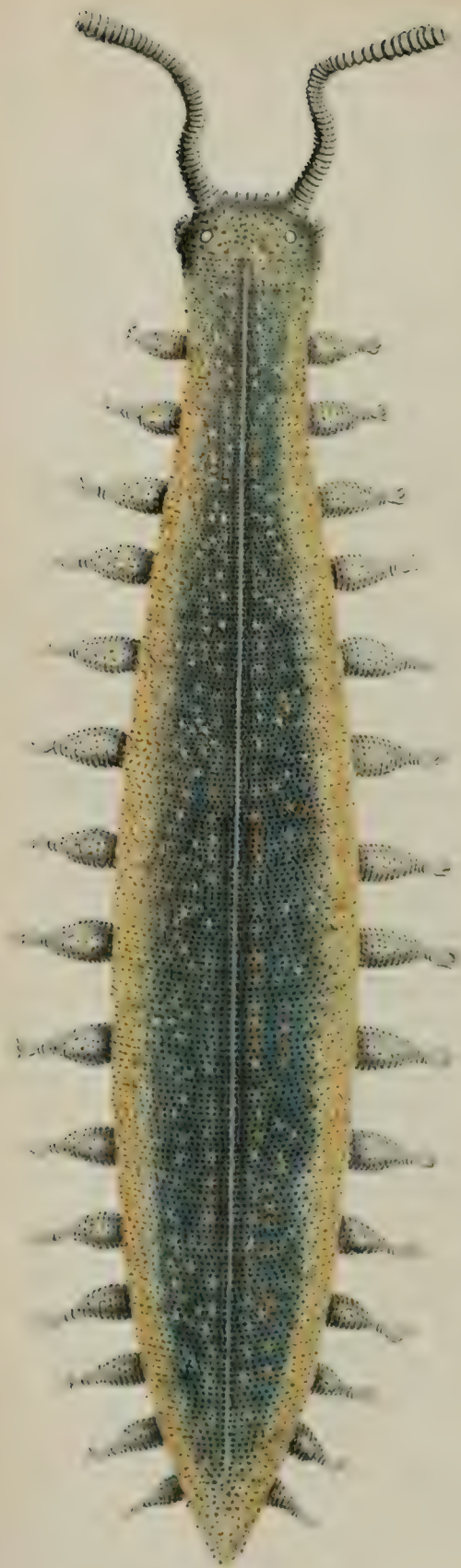
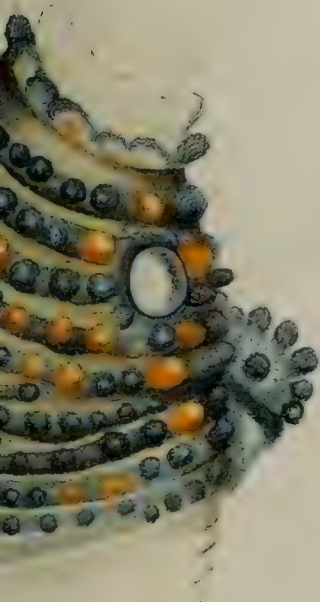


Fig 18



Fig. 20. *Phorus* *Novae Zeelandiae* *M.*  
Fig. 20.



view x 32.



Fig. 21 A



4th leg of *P. Novae Zeelandiae*

Fig. 21.







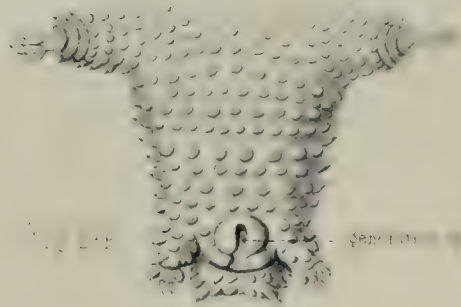


P. Edwardsi. Ventral view of a posterior leg

Generative opening



Ventral view of hind end  
of P. Nova Zeelandiae.



Generative opening

Ventral view of hind end of P. Balfouri.

Fig. 20

Outer blade of jaw of *P. Edwardsii*.

Fig. 21

Inner blade of jaw of *P. Edwardsii*.



Fig. 22

Inner blade of jaw of *P. Capensis*.

Fig. 23

Outer blade of jaw of *P. Capensis*.

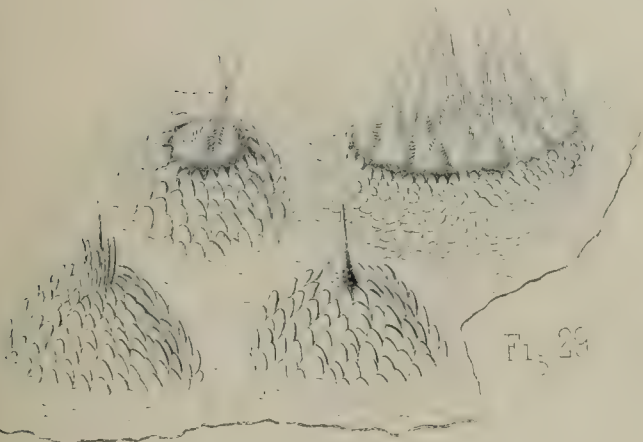


Fig. 25

Skin of leg *P. Trinidadiensis* (Gaffron).

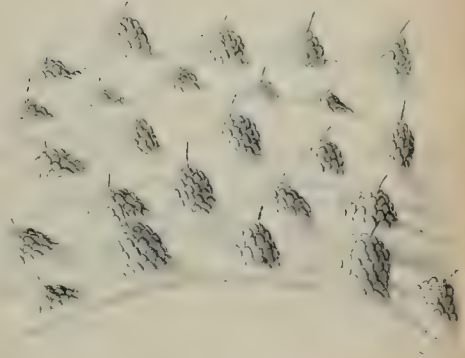


Fig. 26

Skin of *P. Novae-Zelandiae*.





# STUDIES

FROM THE

## MORPHOLOGICAL LABORATORY

IN THE

UNIVERSITY OF CAMBRIDGE.

EDITED BY

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1889



# On the Early Stages of the Development of a South American Species of *Peripatus*.<sup>1</sup>

By

**W. L. Sclater, B.A., F.Z.S.**

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With Plate XXI.

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## CONTENTS.

- I. Introductory Remarks.      |      II. Structure of the Uterus.  
III. Details of the Development.

### I. INTRODUCTORY REMARKS.

THE development of the South American form of *Peripatus* has been worked at by one author only, Kennel, who brought his material from Trinidad. In his two published papers (3) his results are so much at variance with the results arrived at by Mr. Sedgwick (6), who has worked solely at the South African form of the same genus, that it seems worth while to go through the early stages of the South American *Peripatus* again. This I have been enabled to do by means of specimens of *Peripatus* brought home by me alive from Demerara, which have supplied me with a fairly complete series of embryos from the earliest stages onwards.

The species of *Peripatus* occurring in Demerara<sup>1</sup> seems to me to differ materially from the other South American species, as I have pointed out in a note in the 'Proceedings of the Zoological Society' (5). But the absence of well-preserved material makes it very difficult to settle this question with any degree of certainty.

<sup>1</sup> Called by Sedgwick *Peripatus Demeraranus*; vide "Monograph of the Species of *Peripatus*," in Part 2 of this volume of these 'Studies.'—ED.

It will be convenient, however, for me to distinguish the species now under investigation from those treated of by Kennel, and I propose, therefore, to allude to it as *Peripatus imthurni*,<sup>1</sup> since it was Mr. E. F. im Thurn who first discovered *Peripatus* in British Guiana, and it was through his kindness and hospitality that I was enabled to procure my specimens. To Mr. Sedgwick also I owe very many thanks for all his kindness and help to me in my work on this subject. When I arrived in England it was he who preserved the specimens and their embryos, and afterwards helped me with many suggestions, besides allowing me to use all the many resources of his laboratory at Cambridge for the prosecution of my researches.

## II. STRUCTURE OF THE UTERUS.

When the uterus of *Peripatus* is examined it is found to consist of a long and very much coiled duct, which commences at the ovary as a slender tube, and, gradually widening, joins its fellow to form a short vagina, and opens to the exterior at the penultimate somite.

The uterus in the lower part is divided up by constrictions, the space between the constrictions being occupied by an embryo. Advancing towards the ovary the constrictions are longer and the swellings are smaller, till, for some distance from the ovary, the swellings entirely disappear. These swellings mark the position of the various embryos, and are usually eight to ten in number.

The position of the embryos is also marked by deposits of pigment, which appear as a pinky-red colour when seen in the solid uterus; these patches are found not at the actual position of the embryo itself but just in front and behind. In one or two instances, in the case of a very young embryo (*i.e.* the one

<sup>1</sup> In the systematic monograph of the genus *Peripatus* (vide Part 2 of this volume of the 'Studies') the species described by Kennel as *Edwardsii*, and that here called *imthurni* are for reasons stated therein both renamed, the former being called *Trinidadensis*, and the latter *Demeraranus*.—Ed.



nearest the ovary), the pigment was found to envelop it completely, so that it seems that the pigment is first formed all round the embryo, and that it is then gradually divided into two patches, one in front, the other behind the embryo.

The most noticeable point about the uterus of *Peripatus* is that the contained embryos, which are from eight to ten in number, are all at different stages, the youngest near the ovary being perhaps in the segmentation stage, while the oldest will be completely formed and ready to be born.

All my specimens were collected at one season of the year (*i. e.* November and December), so I am unable to say whether they are pregnant all the year round, but it seems probable that this is the case. In this relation *Peripatus imthurni* (*Demeraranus* Sedgwick), as also *P. torquatus* and *Edwardsii*, differs from the South African and New Zealand *Peripatus*, in which cases the development of the embryos, though going on all the year round, commences at one particular season, so that all the embryos found in the uterus of the female are approximately of one age. The structure of the uterus of *Peripatus* will be best seen by examining figs. 1 and 5.

Fig. 1 represents a longitudinal section through a piece of uterus not far removed from the ovary. At *e* is seen a young embryo lying in a cavity of the uterus, this cavity, which is the widened lumen of the uterus, is difficult to trace in front and behind, though in some places remnants of it can be detected; but on the whole it is generally obliterated.

The outer wall of the uterus is formed by a very slightly differentiated single layer of cells (*c.*), which though distinctly nucleated are without cell walls, so that they cannot be separated from one another very easily. Within this is the uterine epithelium, which simply consists of a mass of protoplasm in which is embedded a large number of nuclei. Slight traces of cell walls can be seen in fig. 5, which is a transverse section of a young embryo with its surrounding uterus. The inner line of the uterine epithelium is folded, so that it has a crinkled appearance (*ck.*); this is, doubtless, for the purpose of increasing the absorption surface, and it is by means of this

crinkled appearance that the boundary between the uterus and embryo can be always detected. This folding of the inner layer of the uterine epithelium is not seen very well in the longitudinal section (fig. 1), but it is better seen in fig. 5.

At either end of the embryo is seen a mass of pigment (*pg.*), in the form of black, star-shaped masses, which seem to block up the lumen of the uterus; around and near them are certain darkly-staining irregular masses of protoplasm (*x*), in which no structure whatever can be distinguished. Between the embryos is seen the very curious vacuolated tissue described by Kennel, of which it is very difficult to understand the meaning.

This tissue (*v. c.*) consists of at first a more irregular, afterwards of a more regular mass of vacuoles, separated from one another by thin lines of protoplasm which stain but slightly; along the outer border of these vacuoles there is a line of nuclei (*n.*) which are considerably larger than those of the ordinary uterine epithelium.

The appearance of this vacuolated tissue in transverse section is very well shown by Kennel (Part 1, Pl. VII, fig. 42).

The lines of protoplasm separating the vacuoles run straight from the central point of the section, where occasionally some remains of the lumen of the uterus can be seen, to the circumference where the vacuolated tissue comes in contact with the uterine epithelium. Just at this point, but in the vacuolated tissue, are found the numerous large nuclei generally arranged in a single row (*n.* in fig. 1).

This vacuolated tissue is never found near the embryo; where the embryo is present the vacuolated tissue is entirely replaced by the uterine epithelium, as is seen in fig. 1.

This vacuolated tissue is probably simply modified uterine epithelium, though how the change has been effected I am unable to suggest.

The explanation of this curious histological structure in the uterus of *P. imthurni*<sup>1</sup> seems to me connected with the entire absence of yolk, and the small size of the ovum of this

<sup>1</sup> See foot-note on p. 214.—Ed.

form. The difference in size between the youngest embryo (a sphere measuring .04 mm. in diameter) and the fully formed one, which is often an inch long, is enormous, and there must be a very large quantity of food material absorbed in order to account for this increase in size. This food material must necessarily be derived from the uterine walls, and it appears to me that it is principally derived from these vacuolated regions, and that the pigment and the structureless protoplasm figured *x* are concerned in this phenomenon.

### III. DETAILS OF THE DEVELOPMENT.

The youngest embryos I have found are all of approximately the same age and are in the segmenting stage, but owing to their small size I have never been able to get them, except in a series of sections of unsplit uterus; and in this case the embryo is never so satisfactory, owing probably to the contraction of the uterine tissues due to the action of the reagents.

Fig. 2 represents what I take to be the youngest of all in the segmenting stages; it measures .04 mm. across. It is not easy to assert definitely, but it probably contains eight nuclei embedded in a mass of unsegmented protoplasm, the whole lying free in the cavity of the uterus, which is always present where the embryo is, and for a short distance on either side of it.

In fig. 4, which represents an embryo (.07 mm. in diameter) at a rather more advanced stage, the cells—or rather the nuclei, since there is as yet no sign of any cell partitions—have begun to arrange themselves in a ring round a central cavity. This embryo probably consists of twenty-four cells or rather nuclei. This embryo was also peculiar in that the uterus did not have the masses of pigment usually found in it on either side of the embryo. This embryo measures .08 mm. long by .07 mm. across.

Figs. 3 and 5 are approximately of the same age as fig. 4.

In fig. 5 the uterus has been drawn on one side to show the usual arrangement of the nuclei of the uterine epithelium;



towards the embryo traces of cell outlines can be detected, but in the outer part of the uterine wall the uterus consists simply of a clear protoplasm with dark staining nuclei embedded in it. The nuclei of the uterus stain much more darkly than the nuclei of the embryo itself.

In fig. 3 the only striking peculiarity is the presence of the two bodies (*p. b.*); it seems possible that these may be polar bodies, though beyond their appearance and position I have no further evidence to offer.

Kennel has also figured these early segmenting embryos, and my results do not differ materially from his; he has also figured what he believes to be polar bodies, but in no case do they seem to have separated from the embryo itself, but remain still buried in its substance.

The next stage, which is represented in fig. 6, presents a considerable difficulty; it seems to resemble in some respects fig. 51, Pl. viii, of Kennel.

This embryo (.105 mm. in diameter), which at first I took to be a vesicle with the embryo inside, must, I think, be regarded as a stage previous to the one next to be described, i. e. the pseudogastrula stage.

The embryo consists of a single layer of cells marked out from one another only by their nuclei; it is approximately spherical. The nuclei on one side of the embryo, on being traced out, are found to form a small patch on that side of the sphere, and are considerably larger and more numerous, and it is at this spot, I take it, that invagination will take place.

That this embryo must be placed at this point in the series is evident from the size; as the embryos hitherto described varied from .04 mm. to .08 mm. in diameter, this one (i. e. fig. 4) is .105 mm. in diameter and approximately spherical, while the pseudogastrula, to be described below, is .112 mm. in diameter and .190 mm. in length; this of course forms a fairly regular gradation of increase in size.

The ovum, therefore, of *Peripatus imthurni* is holoblastic, and the segmentation is fairly regular, the result being a blastosphere (fig. 6), that is, a hollow vesicle one cell thick.



There is no sign of any attachment of the embryo to the wall of the uterus, and the inner wall of the uterus is marked by a thickened and crinkled line, which is very characteristic, and which is very useful in later stages for determining the boundary between the embryo and the uterus. The size of the segmenting ova of *Peripatus imthurni*<sup>1</sup> varies from .04 mm. to .07 mm. in diameter, and that of the blastosphere is .105 mm. in diameter.

The next stage, measuring .112 mm.  $\times$  .190 mm., represented in figures 7 A and 7 B, is a most important stage; during it the blastosphere, which was described above, is invaginated so as to form what appears to be a gastrula. I have several series of sections of embryos in this stage, but those figured, which are both from the same embryo, are by far the best; fig. 7 B is a transverse section through the embryo in the middle of its length, showing the invagination; fig. 7 A is a section through one end of the embryo beyond the point of invagination.

The cells are large and generally fairly well defined, more especially the outer layer; in the inner layer it is more difficult to distinguish cell-outlines; the nuclei of the outer layer show a distinct reticulum, and those of the inner layer are rather more chromophilous. The opening of the gastrula is situated on one side of the vesicle, that is, it opens at right to the long axis of the uterus.

This stage, which may be called the pseudogastrula stage, seems to me of great interest, and to be really the key of the whole matter.

The outer layer of the pseudogastrula forms in later stages the wall of the embryonic vesicle; the embryo proper is formed solely from the inner layer of the pseudogastrula.

Of the significance of this stage, and of its relations to the mammalian pseudogastrula, I will say more later on in the final part of the paper.

This stage doubtless corresponds to Kennel's stage, figured in Part I, Pl. viii, fig. 56, where he makes the outer wall of the gastrula *u. e.*, which he interpretes to be uterine epi-

<sup>1</sup> See foot-note on p. 214.—Ed.

thelium; he also letters the point of invagination as *o.*, but neglects to give, as far as I can see, any explanation of *o.*

The result of this is that Kennel throughout his paper considers what I have termed the wall of the embryonic vesicle to be part of the uterine epithelium and a purely uterine structure, whereas to me it seems evident that the wall of the embryonic vesicle has nothing whatever to do with the uterine epithelium, but is derived solely from the outer layer of the pseudogastrula exactly in the same way as the surrounding layer of the mammal's blastoderm, which afterwards forms the chorion, is derived from the outer cells of the Mammalian pseudogastrula.

From the pseudogastrula stage onward the embryo is always found lying in a hollow space, the embryonic vesicle, and attached on one side to the wall of the embryonic vesicle, which is formed from the outer layer of the pseudogastrula stage.

The embryo during this stage is at first sessile, afterwards a stalk is formed; and it is during the formation of the stalk that the two structures termed by Kennel amnion and placenta are found.

Figs. 8 and 11 represent the youngest embryos in vesicles which I have met with.

Fig 11 is drawn from an embryo lying in its vesicle still in the uterus, the uterus has been slightly split and the object drawn after being rendered transparent in benzole. The most noticeable point about fig. 11 is the enormous increase in size of the vesicle which is represented in the previous stage only by the slight split between the inner and outer layers of the pseudogastrula; the embryo, which is seen to form a small dark patch on one side of the vesicle, is oblong in shape and sessile. The size of the embryo is .16 mm. long by .06 mm. across; this is approximately of the same size as the embryo itself in the previous stage; but the vesicle in figure 11 measures .24 mm. across as against .11 mm. in the pseudogastrula stage (fig. 7 B).

Fig. 8 shows a section through an embryo measuring .084 mm. in diameter with part of its vesicle of the same age as fig. 11.

The wall of the vesicle consists of a band of clear protoplasm with definite nuclei at intervals. The embryo itself is composed of two parts, the basal part, in which the nuclei resemble those of the vesicle wall, and the embryo proper, consisting of large cells in which cell outlines can only with great difficulty be distinguished.

These embryonic cells have a very peculiar appearance, due, as it seems, to the diffusion of the nuclear substance or chromatin throughout the cell substance; it therefore follows that no definite nucleus can be detected. Careful focussing, however, seems to indicate clear lines of protoplasm where no chromatin is present, and these lines of clear protoplasm seem themselves to demarcate the various cells of which the embryo is made up.

In the next stage the embryo is still sessile, that is, it is attached to the vesicle wall along its whole length.

Fig. 12 represents an embryo of about this stage, measuring about .1 mm. across, lying in its vesicle, the vesicle again lying in the cavity of the uterus; the two latter have been split open, so as to expose the embryo.

Figs. 9 A and 9 B represent two sections, an embryo and vesicle, of approximately the same size and age as fig. 12; the embryo .14 mm., the vesicle .28 mm. in diameter.

The vesicle wall (*v. w.*) is rather thicker in this stage, and the individual cells composing it are very much better defined than in the previous stages. The embryo proper consists, as before, of large cells with diffused chromatin and obscure cell outlines, and of supporting cells (*sp. c.*), whose nuclei stain very deeply, and whose cell outlines are invisible.

Between the two forms of cells of the embryo there has now appeared a cavity (*o*). This I believe to be arti-fact, and due to the action of reagents, especially as it is very inconstant in its appearance in embryos of this stage.

The only other noticeable feature of this stage is the so-called amnion (*am.*) of Kennel; this consists in the region of the embryo of a few scattered nuclei embedded in strings of protoplasm, in some cases surrounding and fusing with the embryo, in others fusing with the vesicle-wall.



Fig. 9 B represents a section of the same vesicle behind the embryo proper. Here a complete ring of nucleated protoplasm is seen surrounding the space where farther forward would be found the embryo. This is the highest development of the so-called amnion.

The amnion springs from the basal supporting cells of the embryo, as is asserted by Kennel.

This growth, which I have called an amnion, following Kennel's nomenclature, does not seem to me to fulfil the conditions of an amnion at all. An amnion may be described as a double fold of the non-embryonic area of a blastoderm (= vesicle wall), which is caused by the sinking of the heavy embryo into the cavity (= yolk-sac or vesicle) filled with fluid, the double folds finally fusing at the top.

This definition is true both for the amnion of the vertebrate and of the insect. In the case of *Peripatus* the outgrowth is not a double fold, but a single and thin lamina of protoplasm; it cannot possibly be explained by the mechanical descent of the embryo into the vesicle, since in that case the amnion would be formed on the other side of the embryo from folds in the vesicle wall.

It seems, therefore, that this so-called amnion of *Peripatus* has no sort of homology or analogy to the true amnion of insects and vertebrates. As to the use of this structure in *Peripatus*, it is at present impossible to dogmatize, but it seems to me that, like other embryonic organs, it has some part in the conveyance of nourishment to the embryo from the vesicle and uterus.

Another embryo—measuring the embryo .12 mm. the vesicle .25 mm. respectively—of about the same size and age as the one above described, is represented in fig. 10; it is remarkable for the thinness of the vesicle wall, which consists of a quite slender string of protoplasm with very few nuclei. This and several other examples which I have met with, of the same sort seem to show that the vesicle wall varies much in thickness at different times.

During the next stage the primary layers begin to form, and



soon after that the legs begin to grow out, and the embryo begins to assume the form of the adult.

Figs. 13, 14 A, and 14 B represent whole embryos at this stage. Figs. 14 A and 14 B are drawn from the same embryo, the latter by reflected light, and made transparent by benzole, the former by direct light in alcohol; fig. 13 is also drawn with reflected light.

Figs. 14 A and 14 B represent an acorn-shaped embryo corresponding to Kennel's fig. 12, lying in the unbroken embryonic vesicle; the band across the embryo and the shaded part of fig. 14 A, from which springs the stalk of the embryo from the thickened area of the vesicle wall, called by Kennel the placenta. The stalk, which is represented only in fig. 14 B, is drawn too slenderly; it should be considerably thicker.

The other embryo (fig. 13) resembles fig. 14 in every way, except that it has not been removed altogether from the uterus, of which the split half is still seen attached to the vesicle.

These embryos both measure .24 mm. across, and the vesicles are respectively .8 mm. and .6 mm. long.

When the embryo has got to this stage the layers begin to be differentiated. The mesoderm and endoderm are formed by a proliferation of cells which takes place at what will afterwards be the hind end of the embryo.

This process is illustrated in figs. 15 A, 15 B, and 15 C, which all represent sections from different parts of one embryo; fig. 15 A being at the hinder end and fig. 15 C towards the front end of the embryo. These figures show the embryo proper alone, neither stalk nor vesicle wall have been represented.

In fig. 15 A the embryo is seen to consist of a double layer of long-oval nuclei (*ec.*), from which are afterwards formed the ectoderm cells, and from which at one point (*pr.*) there is a proliferation of cells (*en.*) filling up the greater part of the cavity of the embryo; from these cells the endoderm and mesoderm are subsequently formed; the endoderm cells have a more granular and more rounded appearance than the ectoderm cells.

Fig. 15 B shows the appearance of the same embryo some-

what further forward; here all connection between the endoderm and ectoderm is lost, and the endoderm is growing forward in the middle of the embryo at the expense of the proliferating cells behind.

In fig. 15 c, still farther in front, a cavity (*mes.*) begins to appear in the hitherto solid endoderm; this is the first commencement of the enteron.

Farther still in front the endoderm thins out somewhat, so as to form a narrow thin band encircling the enteron; still farther it gradually disappears, so that nothing is left at the extreme head end of the embryo but the ectoderm. From these proliferated cells the mesoderm is also formed later on. Another feature of this stage is the thickening of the ectoderm on one side, or rather, ventrally to form the nerve-cord. This is not marked at the hind end of the embryo, where the thickening extends all round, but is more marked at the front end (fig. 15 c), where on one side the ectoderm is seen to consist of a double layer (*n. c.*), on the other of only one; it is from part of this double layer that the nervous system will be subsequently formed.

The proliferation of cells takes place on the ventral side of the embryo distally to the stalk, which is attached to the dorsal side of the embryo at the head end. This proliferation, therefore, exactly corresponds to the primitive streak of *P. capensis* as described by Sedgwick; and all that has to be conceded is that in consequence of the extraordinary changes in the early stages due to the small size of the ovum and the absence of yolk, the blastopore of *P. capensis* described by Sedgwick has disappeared from *P. imthurni*,<sup>1</sup> although its position is still marked by the primitive streak, which replaces the primitive streak + the blastopore of *P. capensis*.

After this stage I have not worked at the development of this form; for one reason I have not had time, for another because the later stages seem to me to resemble those of *P. Edwardsii*<sup>1</sup> and *P. capensis* as arrived at by Kennel and Sedgwick respectively.

<sup>1</sup> See foot-note on p. 214.—ED.

The organ described by Kennel as a placenta does not appear till somewhat later. I shall not call it a placenta, because it does not seem to me to bear any analogy to the mammalian placenta.

It seems to me that the best words to express the organs are the embryonic and vesicular thickening corresponding to the two parts of the placenta of Kennel (i. e. embryonic and uterine placentas).

An early stage in its development is shown in fig. 16, which represents part of the vesicle wall of a stage of the same age as fig. 15; here it is seen to consist of a large mass of cells (*pl.*) formed by the proliferation of the wall of the vesicle, which under ordinary circumstances consists of a single row of cells only. This is the vesicular thickening (= uterine part of the placenta) as distinguished from the embryonic thickening (= the embryonic placenta), which is merely the swollen part of the vesicle wall from which the stalk of attachment arises (*z.*).

The vesicular thickening is found in its fullest development rather towards the hinder end of the embryo, whereas the stalk of attachment and its swollen base are at the head end of the embryo.

The histological structure of the vesicular thickening at this stage is not remarkable; it consists of a mass of nucleated cells. The outlines of the cells are very apparent, and their protoplasm is in parts much vacuolated.

This stage corresponds in age to the embryo last described (fig. 15), and is the earliest stage at which the vesicle swelling is of any great size or importance.

Fig. 17 shows a much further development of the vesicular thickening; owing to its large size only a small portion of the vesicle wall (*v. w.*) is represented.

The histological structure of the vesicular thickening has here completely changed, all traces of cell walls have disappeared, the nuclei are darker and more distinct, and the protoplasm presents a very peculiar granular appearance which I have not seen elsewhere.

The vesicular thickening seems to be fused to the uterus wall

itself, but of this I am not certain, since in all my sections the uterus wall has been in each case separated from the vesicle wall, and on opening the fresh uterus the vesicle always comes away by itself.

The meaning of the cells marked *f* in fig. 17 has puzzled me; I think it highly probable that these nuclei and their adjacent protoplasm are food material for the embryo lying in the vesicle (not shown in the fig.), since the nuclei resemble nuclei found in the embryo, and the mass of cells, if followed through adjacent sections, are found to form a patch or cap of cells lying on the vesicular thickening; the vesicular thickening itself is seen when followed out to be directly continuous with the vesicle wall, so that the theory that the patch of cells (*f*) is merely a continuation of the vesicle wall, and the vesicular thickening (*pl.*) a product of the uterine epithelium, seems to me untenable.

This vesicle swelling persists till quite the end of the uterine life of the embryo as a thickening at the hinder end of the embryonic vesicle.

The placenta in the case of mammals is a vascular plexus formed by the uterine epithelium, which is in connection with a vascular plexus formed by part of the embryonic membranes.

In the case of *Peripatus imthurni* (Demeraranus Sedgwick), there is certainly, as far as I have been able to observe, no plexus of blood-vessels at all; and Kennel, I think, makes no mention of this matter.

But apart from that, since it may be argued that the word placenta can be applied to any uterine nourishing organ, whether vascular or non-vascular, the swelling of *Peripatus* is altogether an embryonic organ, the uterus takes no part in its formation whatever.

The vesicular thickening of *Peripatus* is formed entirely by the proliferation of the cells of the wall of the embryonic vesicle, which vesicle is originally derived from the outer wall of what I have called the pseudogastrula, so that it has nothing whatever to do with the wall of the uterus.



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## EXPLANATION OF PLATE XXI

Illustrating Mr. W. L. Sclater's Memoir, "On the Early Stages of the Development of the South American Species of *Peripatus*."

*Complete List of Reference Letters.*

*am.* So-called amnion. *c.* Cuticular layer. *ck.* Folded inner edge of the uterine epithelium. *e.* Embryo proper. *ec.* Ectoderm. *en.* Endoderm. *f.* Cells of doubtful function, probably nourishing. *mes.* Mesenteron. *n.* Nuclei of vacuolated epithelium. *n.c.* Nerve-cord. *o.* Artificial cavity due to reagents. *p.b.* Polar body. *pg.* Pigment. *pl.* Vesicle swelling (placenta). *pr.* Primitive streak. *sp.c.* Supporting cells. *u.e.* Uterine epithelium. *ut.* Uterus. *v.* Vesicle. *v.e.* Vacuolated epithelium. *v.w.* Vesicle wall. *z.* Embryonic swelling (embryonic placenta) whence the stalk arises.

All the figures, except Figs. 1 and 11 to 13, are drawn with Zeiss's camera obj. D, oc. 2), but Figs. 16 and 17 have been reduced to one half the original size.

FIG. 1.—Longitudinal section through the upper part of the uterus, showing a young embryo and the curious histological structure of the uterus. Drawn with Zeiss's camera. (Obj. A, oc. 2.)

FIG. 2.—Youngest embryo met with, measuring .04 mm. in diameter. It seems to consist of eight nuclei with surrounding protoplasm.

FIG. 3.—Embryo segmenting rather more advanced with polar bodies.

FIG. 4.—Embryo with commencing central cavity.

FIG. 5.—Segmenting embryo drawn with the surrounding uterus to show the structure of the uterus and its relation to the embryo.

FIG. 6.—Young blastosphere stage before gastrulation and after the completion of the segmentation.

FIGS. 7A and 7B.—Two sections of an embryo in the pseudogastrula stage. Fig. 7A shows the condition of the embryo at one end beyond the influence of the invagination; Fig. 7B is a transverse section through the gastrula and its blastopore.

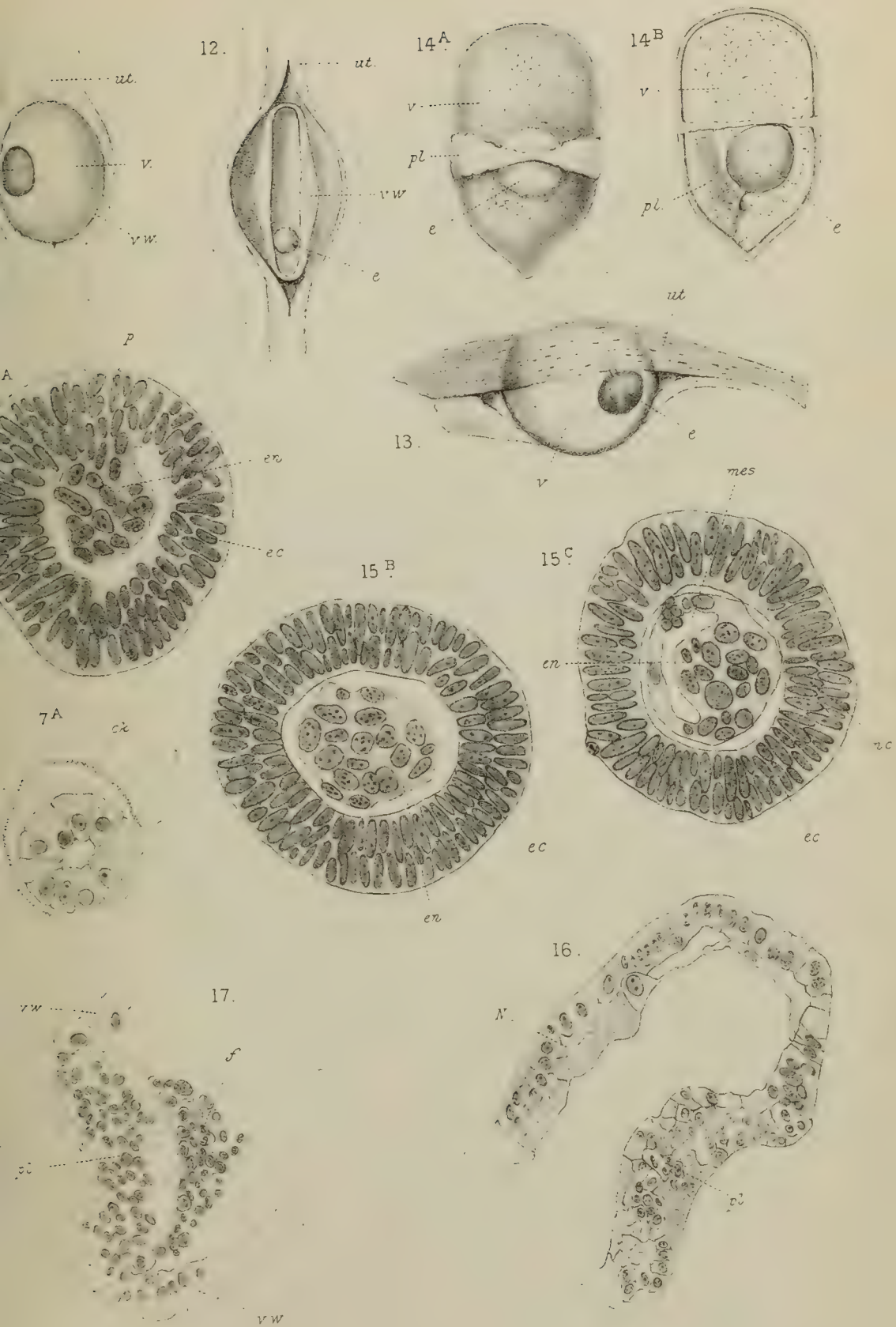
FIG. 8.—Youngest embryo found in a vesicle. The wall of the vesicle is much broken, only a very small part being represented in the figure.

FIGS. 9A and 9B.—Two sections through a vesicle and embryo of moderate size. The embryo is still sessile. Fig. 9A represents a section through the











middle of the embryo, and shows the so-called amnion in part and the supporting cells (*sp. c.*); Fig. 9B is cut through the vesicle behind the region of the embryo, and shows the amnion at its highest development.

FIG. 10.—Section through an embryo of almost the same age as Fig. 9, probably a little older. The vesicle wall in this case is reduced to a very thin string of protoplasm with a few nuclei embedded in it.

FIGS. 11, 12, 13, 14A and 14B are drawings of solid embryos; in the case of Figs. 11, 12, and 13, lying in the uterus, which has been split open to expose them; in the case of Figs. 14A and 14B the embryo has been removed from the uterus. All, with the exception of Fig. 14A, have been drawn with a Zeiss A after being made transparent by soaking in benzole. Fig. 14A was drawn when lying in absolute alcohol by refracted light.

Fig. 11. Stage about the same age as Fig. 8. The embryo is entirely sessile; there is no sign of a stalk. The embryo measures .16 mm.  $\times$  .06 mm.

Fig. 12. Stage of about the same age as Figs. 9A and 9B. The embryo is shown lying in the vesicle, which is in turn shown lying in the uterus; both uterus and vesicle having been split open.

Fig. 13. A stalked embryo in a vesicle, the vesicle lying in the split uterus. Embryo measures .24 mm. long.

Figs. 14A and 14B. The same embryo, drawn, the former by refracted, the latter by reflected, light; Fig. 14A a ventral view, Fig. 14B a side view; show a vesicle with an acorn-shaped embryo lying within it. The embryo is stalked, the stalk springing from the darker area (so-called embryonic placenta). The embryo measures about .24 mm. across.

FIGS. 15A, 15B, and 15C.—Three sections through different parts of the same embryo. Fig. 15A is the posterior of the three, Fig. 15B the middle one, and Fig. 15C the most anterior. Fig. 15A shows the primitive streak (*pr.*), Fig. 15B the clump of cells growing forward from that point, Fig. 15C the commencing mesenteron.

FIG. 16.—Part of the vesicle wall of an embryo of the same age as Fig. 15, showing the commencement of the formation of the so-called placenta.

FIG. 17.—Later stage in the development of the placenta.

# On the Development of *Peripatus Novæ-Zealandiæ*.

By

**Lilian Sheldon,**

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## PART I.

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With Plates XXII, XXIII, XXIV, XXV and XXVI.

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THE account to be given in this paper is unfortunately by no means a complete one, owing to the difficulties attendant on working at the subject in this country. The great drawback is the difficulty of obtaining the creatures, and as, so far as I know, there is no way of keeping them alive in England, it is necessary to kill them and remove the embryos as soon as they arrive, so that one is by no means certain of obtaining the stages which are required, when one does have the good fortune to obtain a supply of the creatures.

All the embryos which I have worked upon were given to me by Mr. Sedgwick, and most of them were taken out of the uterus and preserved by him before he handed the material over to me. So far we are not able to state at what times of the year the different events in the development take place, but it is possible nevertheless that there may be a definite sequence, as we have at present only received the material in December, July, and April, and so have not many data to go upon.

The material which arrived in July contained seven females; three of these were without embryos in the oviduct or uterus, and the other four contained embryos varying in age from that



figured in figs. 25 and 26 to those which were just ready to be hatched.

The second supply arrived in November, but most of the creatures were not opened till December. One female, which was opened on November 27th, contained several fully developed embryos, while in one opened on November 30th the uterus was empty. Seven females which were opened in the middle of December contained only unsegmented and segmenting ova in their uteri.

In the last supply, which arrived last April, there were nine females, which were opened on the 18th day of the month. Of these five had no embryos in the uteri, one had several old embryos, one segmenting ovum, and two embryos, one of which is shown in sections in fig. 15; another contained several old embryos, one segmenting ovum (which is shown in section in fig. 11), and two of the stage represented in fig. 17; another contained the embryos, sections of which are shown in figs. 13, 18, 19, and 20, and also one unsegmented and several segmenting.

The New Zealand species, like all the others which are so far known, is viviparous, the embryos undergoing the whole course of their development in the uterus of the mother.

The ripe ovum is very large as compared with those of *Peripatus capensis* and *P. Edwardsii*, measuring about 1.5 mm. in its long axis. This large size is due to the enormous amount of food-yolk with which the egg is charged.

The egg is enclosed in a thick tough shell, which in the fresh state adheres closely to it; after treatment with certain reagents it becomes somewhat distended, and can be pricked or removed. This is especially the case with eggs which are preserved in hot corrosive sublimate, which causes the shell to swell up, to become less tough and to lie at a greater distance from the egg, so that it can be quite easily removed without damaging the surface of the egg. This is not so easily accomplished in cases where the corrosive sublimate was not heated, and the surface of several of my eggs was more or less injured in the process of removing the shell. It is necessary to prick

the egg-shell before placing the eggs in spirit, as otherwise it collapses and crushes the embryo. Before cutting sections of the eggs I almost always removed the shell, since it was too hard to cut well, and was also apt to prevent the paraffin from penetrating the ovum.

Within the shell the ovum is enclosed in a vitelline membrane, which adheres closely to it, and is thin and membranous. The two are easily distinguishable in eggs stained with picrocarmine, as the shell stains yellow and the vitelline membrane red.

The only accounts which have been hitherto published of the development of *P. novæ-zealandiæ* are by Hutton<sup>1</sup> and Kennel,<sup>2</sup> both of which are very brief. These observers state that the segmentation is holoblastic, which is not the case, it being rather on the centrolecithal than on any other type of segmentation.

#### METHODS.

The most satisfactory preparations obtained were from eggs which were preserved in hot or cold corrosive sublimate and glacial acetic acid mixed in the proportion of two to one. Other ova were preserved in Kleinenberg's picric acid, but these were not satisfactory. The eggs were all stained in picrocarmine, and afterwards passed through the various strengths of alcohol in which a small amount of picric acid was dissolved; by this method the yolk is stained yellow, the protoplasm light, and the nuclei deep red, so that they are easily distinguishable from one another. I am indebted to Mr. Harmer for the knowledge of this method.

The embryos were all removed from the uterus in the living state, and were preserved at once.

I do not purpose in this paper to enter into the subject of the ovarian ovum and the changes undergone by it in its

<sup>1</sup> Hutton, Capt. F. W., "On *Peripatus novæ-zealandiæ*," 'The Annals and Magazine of Natural History,' 4th Series, Nov., 1876.

<sup>2</sup> Kennel, Dr. T., "Entwicklungsgeschichte von *P. Edwardsii*, Blanch, und *P. torquatus*, n. sp.," 'Semper's Arbeiten,' Band vii, 1885.

passage into the ovum with the segmentation nucleus, as I hope to be able later to make some further investigations on that subject. It will be enough to state here that in several cases there were ova in the uterus which possessed no nucleus whatever; there was a small amount of protoplasm present as a very loose and not always easily-recognisable reticulum lying among the yolk-spheres. This protoplasmic reticulum was sometimes scattered throughout the egg, but was more often only present at the periphery; while in some cases it was aggregated at one point only. In one ovum there was a very large compact mass of protoplasm at one point near the periphery, but no trace of a nucleus could be discerned.

#### SEGMENTATION.

Immediately before the segmentation begins the ovum consists of a great mass of yolk-spheres, and contains a single nucleus. The position of the nucleus in the ovum varies somewhat in different cases; in fig. 1 it is seen to be situated at some distance from the periphery of the ovum; in this case it is round in form, and contains a deeply staining wall and also a single mass of chromatin. The protoplasm in which it is embedded is compact and dense, and contains at its periphery several chromatin particles. In the ovum from which fig. 2 is taken the nucleus and its surrounding protoplasm had a somewhat different position and form. The nucleus is situated near the periphery of the ovum, being separated from the vitelline membrane by only a thin layer of yolk. The nucleus has a peculiar lobed form, and consists of three masses of deeply staining material, between which is a portion of nuclear substance which stains less deeply. It is surrounded by a very small amount of protoplasm, which forms a loose reticulum, the strands of which pass in and are lost among the yolk-spheres.

The next stage is that in which two nuclei are present in the egg; two sections from such an egg are figured in figs. 3 *a* and 8 *b*. One nucleus is situated at the periphery of the ovum and the other somewhat deeper, but both lie in the centre



of one of the long surfaces on the same side of the ovum, and each is surrounded by a protoplasmic area. The peripherally-situated nucleus had a peculiar lobed form, while the other seemed to be in the act of dividing, the chromatin particles representing the spindle-fibres cut through transversely. In another ovum, in which two nuclei were present, both were situated quite near the periphery; but in this case the sections were too thick for the structure of the nuclei to be made out.

In the next stage, in which three nuclei are present, other changes have also taken place in the ovum. These concern the segmentation of the yolk. At the pole where the nuclei are situated the yolk is broken up into segments, which vary considerably in shape and size. The yolk-spheres at this pole are smaller than those over the rest of the egg. The yolk segmentation does not bear any definite relation to the protoplasmic and nuclear segmentation, but takes place quite independently of it. A nucleus is present in each of three of the yolk-segments, in others there is a considerable protoplasmic reticulum, but no nucleus, while in others again there is no trace of either protoplasm or nucleus. The nuclei are all situated near together. Fig. 4 *a* is a section through the whole egg. The section passes through one nucleus which is round in form and contains a chromatin network, and is surrounded by an area of protoplasm. It is situated in a yolk-segment, the spheres composing which are very small. The section passes through several other yolk-segments, four of which contain no recognisable protoplasm or nucleus; another, which is not completely segmented off from the mass of the yolk, contains a small compact mass of protoplasm. The greater part of the yolk is unsegmented, and is composed of very large yolk-spheres. In future that part of the surface of the ovum at which the nuclei are situated will be spoken of as the protoplasmic area. Figs. 4 *b* and 4 *c* are taken from other sections through the same egg, and represent sections of the protoplasmic area seen under higher power. In fig. 4 *b* there is a considerable amount of protoplasm in two of the yolk-segments besides that in which the nucleus is present. The nucleus is



embedded in a large mass of protoplasm, and is very much lobed in form. In fig. 4 *c*, which passes through the third nucleus, two of the yolk-segments possess a small amount of protoplasm, and there is a very large amount in the segment which contains the nucleus. The nucleus itself is very peculiar in shape, and is made up of a large number of lobes.

At the next stage the yolk is segmented throughout the whole egg, but the nuclei are still confined to the protoplasmic area. In the fresh state the yolk-segments are very clearly seen over the whole surface, so that in a view of the whole egg it appears to be made up of a number of round segments, all resembling one another in size and shape; a surface view of such an egg is figured in fig. 23. It is this appearance which probably led Hutton and Kennel to state that the segmentation was holoblastic, but the fact that it is only due to the yolk segmentation is quite clear when sections of the egg are examined.

The yolk-segments are much smaller at the protoplasmic area, and the yolk-spheres composing them are also smaller than they are over the rest of the egg.

The protoplasm is still mainly confined to the protoplasmic area, but small quantities are present in other regions; it consists of a reticulum very indefinitely segmented, the whole being intimately connected by strands passing over from one aggregation of protoplasm to another. Nuclei are scattered about very irregularly through the protoplasm, in some places two or three lying close together, while in others there is a considerable tract of protoplasm devoid of any nucleus. Sections through the protoplasmic area of such an egg are shown in figs. 7 *a* and 7 *b*.

A surface view of an egg slightly older than the preceding is shown in fig. 24; the yolk segmentation on the surface of the egg has been obliterated in the course of preservation, but at the protoplasmic area the segments are clearly seen, the presence of the protoplasm having rendered the surface at this point less easily disintegrated. This egg bears a very close resemblance to those figured by Mr. Sedgwick in the first part

of his work on the 'Development of *P. capensis*' (fig. 7). A section through the protoplasmic area of this egg is shown in fig. 5. The protoplasmic masses, which in surface view appeared to be separate from one another, are seen to be very closely connected by strands; in two places two nuclei are seen lying close to one another, and in another a single nucleus is cut through. The yolk, situated below the protoplasm, is segmented. Fig. 6 represents a section of a small portion of the protoplasmic area drawn under higher power, in which a large number of nuclei are crowded close together in a small area of reticulated protoplasm.

In the next stage the protoplasmic segments with their nuclei extend over a somewhat larger area of the surface of the egg, the nuclei being still very irregularly scattered through the protoplasm. This extension of the protoplasm is shown in fig. 8, which is drawn from the protoplasmic area of a section of this age. The segments are rather more distinct from one another than they are in the eggs so far described, but they are still connected by protoplasmic strands. The yolk is very definitely segmented. Fig. 9 is from a section through an egg of about the same age; in it the protoplasmic segments are much more distinct than is usually the case at this stage.

In all the above-described stages many of the nuclei show indications of karyokinetic figures, so that it is probable that all the nuclei are derived by division of the first segmentation nucleus, and it is not necessary to suppose that any process of free-nuclear formation has taken place.

In the latest segmentation stage which my material has provided the protoplasmic segments extend over rather more than half the surface of the ovum. They are arranged in a regular layer near the periphery, and appear to be more definitely separated from one another than in the previous stages, although it is probable that they are connected by strands which are hidden by the yolk which separates them. Nuclei are present in many of the segments, although some are devoid of them. In the centre of the protoplasmic area

there is a mass of protoplasm lying quite on the periphery, and extending over it for a small area. In it there is a large round nucleus with very evident traces of a karyokinetic figure. Small irregular branched masses of protoplasm are present near the periphery at the lower side of the egg, but they contain no nuclei. In the centre of the egg there are two or three very definite protoplasmic masses, none of these contain nuclei, but in one there are three very definite chromatin granules. Fig. 10 represents a section through this ovum.

Between the last-described ovum and the next one which I have, there is a considerable gap. In this ovum, a section through which is represented in fig. 11, the yolk is still segmented, and nuclei are present scattered irregularly throughout the ovum, being more plentiful near the periphery than towards the centre. In one region there is a special aggregation of nuclei lying in a loose protoplasmic reticulum; this mass of nuclei is situated on one surface of the egg, its long axis being parallel to the long axis of the latter, and extending through about the middle third of its length. In transverse section it is irregularly triangular in shape, the apex being directed towards the centre, and the base forming the periphery of the egg in this region. The protoplasmic reticulum passes without any sharp line of demarcation at its edges into the yolk. Fig. 12 represents the protoplasmic portion of the ovum; it is drawn from the same section as fig. 11, but under Zeiss' obj. D instead of obj. A. The nuclei vary much in size, and some stain very much more deeply than others; they are extremely irregularly arranged, there being in some places a group of several crowded close together in a small area of protoplasm; this is very noticeable in one place in fig. 12, where eleven small nuclei lie together in a small oval mass of protoplasm; in other places they are much farther apart, and sometimes there is a fairly large area of protoplasm devoid of nuclei. A few yolk-spheres are present among the meshes of the reticulum. There is no trace of any cell boundaries, the protoplasm forming a very loose reticulum, the whole mass being everywhere connected together by strands. The impos-



sibility of fixing cell limits is rendered still more obvious by the irregular arrangement of the nuclei. Traces of a chromatin network, more or less distinct, are visible in most of the nuclei; the smaller ones as a rule stain more deeply than the larger.

A section of an ovum of the next stage is figured in fig. 13, in it the reticulum of the protoplasmic area has become much more compact, and is flattened against the surface of the egg. At the same time its width laterally has increased, so that it spreads over a larger surface at the periphery of the egg. In fact the protoplasmic area might be described as forming a flattened plate on one surface of the ovum, throughout rather more than one third of its length; the lateral edges of the plate show a slight tendency to turn inwards away from the periphery of the egg. A trace of the triangular shape presented by the protoplasmic area in the last stage still persists in a low pointed ridge which runs along the middle of the plate, and projects inwards towards the centre of the ovum. Fig. 14 represents the protoplasmic area, it is drawn from the same section as fig. 13, but under a higher degree of magnification. In it the protoplasm is seen to consist of a fairly close reticulum, in which the nuclei are packed very near together. The nuclei themselves possess the same characters as those shown in fig. 12, and like them are of various sizes. There is still no trace whatever of any cell divisions, the protoplasm forming a continuous mass in which the nuclei lie quite irregularly. The tendency of the lateral edges of the plate to turn inwards is shown in this figure. Nuclei are still present scattered through the yolky part of the ovum, and, as in the last stage, are more numerous towards the periphery. Traces are visible of the segmented character of the yolk, but this is not very clearly shown owing to the yolky part of the egg having broken and fallen out to some extent in the course of cutting the sections.

Between this stage and the one now to be described there is again a large gap. A transverse section through the middle region of the egg is shown in fig. 15 *c*; in it the appearance is



as follows:—The egg is bounded externally by the vitelline membrane (*v. m.*); beneath this and closely applied to it is a peripheral layer of yolk (*p. y.*), in which are present a number of small round, highly refractive bodies, which stain very deep red with picrocarmine. Within this peripheral yolk layer and forming a ring round the egg is a thin layer of protoplasm (*Ec.*), with clearly defined inner and outer boundaries, and a single layer of nuclei arranged regularly in it. At one point there is a great proliferation of nuclei forming a conspicuous mass (*p. n.*) on the outer side of the protoplasmic ring; its boundaries are not very sharply defined, so that it passes at its edge into the yolk without any clear line of demarcation separating the two. The space inside the ring of protoplasm is filled with yolk.

In passing through the series of sections from the middle one just described towards one end of the egg, the proliferating mass of nuclei is found to gradually thin out, and finally disappear, so that, as is shown in fig. 15 *d*, the protoplasmic band (*Ec.*) comes to be of the same thickness along its whole circumference. At the same time the diameter of the ring gradually diminishes, and it finally ends not far from the extremity of the egg as a cul-de-sac, the blind end of which is enveloped in the peripheral yolk.

Passing from the central section towards the other end of the egg, the proliferating mass of nuclei increases in size, and then becomes divided into two masses (vide fig. 15 *b*, *p. n.*). These masses are not completely separated from one another, but are connected above and below by a layer of protoplasm, in which nuclei are present, so that a second cavity is produced (fig. 15 *b*, *p.*) lying below that enclosed by the protoplasmic ring, and bounded laterally by the proliferating mass of nuclei, and above (*Sep.*) and below by the bands of protoplasm which connect these together. Near the extremity of the egg both these cavities end blindly, the secondary one, i. e. that which lies between the proliferating masses, ending a little before the original cavity. The blind end of the latter is enclosed in the peripheral yolk, which at this end of the eggs shows signs of

the original yolk segmentation, and contains a good many nuclei (fig. 15 *a*).

Cell outlines are not distinct at this stage, but indications of them are present between the nuclei of the protoplasm bounding the sac. There are no traces of any cell boundaries in the proliferating mass of nuclei.

The structure of the egg at this stage may be briefly described as follows:—The egg is surrounded by a vitelline membrane; beneath this is a peripheral layer of yolk containing small round, highly refractive bodies; within this is a sac ending blindly at both ends, bounded by a layer of protoplasm, which is one cell thick, except along one line, where, throughout most of its length, there is a longitudinal ridge composed of a mass of proliferating nuclei, among which many of the small round, highly refracting bodies are scattered. At one end this ridge thins out and gradually disappears; towards the other it increases in thickness, and by the parting of its lateral walls comes to enclose a secondary cavity, which lies below the primary sac, and ends blindly shortly before the latter. The sac is filled with food yolk, in which a few scattered nuclei are present.

By a comparison of this embryo with those of later stages it is found that the internal sac, together with the proliferating ridge, represents the embryonic part of the ovum, the single layer of protoplasm being the ectoderm of the embryo. The mesoderm and ectoderm are not yet definitely differentiated. The peripheral yolk does not form any part of the future embryo, but seems to be absorbed as food material.

The most tenable hypothesis, whereby this stage can be connected with the previous one, is that the cells at the edges of the protoplasmic plate of the latter grow round the ovum in a normal epibolic manner, except that, instead of spreading over its surface, they grow round slightly internal to it, so as to leave a peripheral layer of yolk outside them. A small quantity of this peripheral yolk inserts itself between the protoplasmic plate and the vitelline membrane, so that the whole embryo is surrounded by yolk. The protoplasmic plate itself probably

forms the proliferating ridge. The small round, deeply staining bodies found in the peripheral yolk have no obvious rudiment in the previous stage; they present no definite structure, and, except for their property of staining deep red with picrocarmine, they resemble the yolk-spheres. It is possible that they may be derived by the breaking down and alteration of the nuclei which were present in the yolk in the previous stage. This view as to their origin is supported by the fact that they are very much more numerous in the peripheral than in the central yolk, which was also the case with the nuclei. Whatever their origin may be, they probably function as food material, as to a certain extent at this stage, and very largely in later ones, they are found lying among the cells of the embryo.

By the next stage again the ovum has undergone considerable changes; the peripheral yolk is mostly absorbed, but the small round bodies are still very numerous, lying both outside the embryo, i. e. between it and the vitelline membrane, and also among the cells of the embryo, thereby rendering the exact boundaries of the latter difficult to distinguish. In a transverse section through the egg, near its anterior end, the embryo is seen as a sac surrounded by a layer of ectoderm, which is rendered somewhat indefinite by the intrusion of the small round bodies. At the ventro-lateral corners there is a pair of proliferating masses of nuclei, which are the rudiments of the præoral lobes. As in the last stage, the whole embryo is filled with yolk. A section slightly posterior to this is shown in fig. 17 *a*; in it the rudimentary præoral lobes (*p. o. l.*) are present, though they are rather smaller than they were in the section last described; lying between them, on the ventral face of the embryo, is the transverse section of the tip of a small second sac (*post. Em.*), which is bounded by a fairly definite layer of nuclei, and contains in its interior yolk-spheres, small round bodies, and a few large nuclei. In a section through the middle region of the ovum, such as is figured in fig. 17 *b*, the second sac is found to have increased in diameter, and to lie on the ventral face of the primary sac, from which it is separated by a protoplasmic septum. Proliferating masses of



nuclei (*Mes.*) are present at the ventro-lateral corners of the primary sac, and there are also indications of a proliferation of the nuclei at those corners of the secondary sac which are apposed to the thickenings on the primary one.

In a section through the posterior region of the egg (such as is represented in fig. 17 *c*), the septum dividing the two sacs from one another has disappeared, so that they are in free communication with each other. Thus the central cavity of the embryo is continuous from the anterior extremity of the embryo round the posterior end of the egg to the tip, which was found lying on the ventral face of the head of the embryo between the præoral lobes (vide fig. 17 *a*, *post. Em.*) The longitudinal thickenings along the ventro-lateral borders of the sacs coalesce shortly behind the point where the septum disappears; that is, the thickening on the right of the primary sac coalesces with that on the right of the secondary one, and similarly those on the left; so that on each side of the embryo there is a thickened ridge which starts just behind the præoral lobes, and is continued round behind the septum along the sides of the ventral sac. These thickenings are the mesoderm. The endoderm is only represented by a few scattered cells in the yolk which fills the embryo. The embryo, therefore, consists of a sac which, except at the posterior end of the egg, is divided into a dorsally- and a ventrally-lying one by a longitudinal horizontal septum. The whole embryo is filled with yolk, and is surrounded by a thick layer of the small round bodies, outside which is the vitelline membrane.

Several intermediate stages are obviously wanting between this embryo and the previous one, and it is therefore not possible to state positively how the one develops into the other. It seems possible, however, that the cavity (figs. 15 *b*, *p*) which was present in the proliferating mass of nuclei in the previous stage, corresponds to that which constitutes the ventral sac in the anterior portion of the egg last described (fig. 17 *a*, *post. Em.*). If the proliferating mass were anteriorly to divide completely, only remaining attached by a string of cells on the ventral surface of the embryo, constituting the ventral ectoderm,



a condition would be attained similar to that found at the extreme anterior end of the embryo, the now paired proliferating masses being the præoral lobes. Farther back the condition would be similar to that found in fig. 15 *b*, in which the proliferating mass has divided centrally, but the divided masses remain connected above and below by a string of cells, so as to enclose a secondary cavity lying on the ventral face of the primary one, the two being separated only by a thin layer of protoplasm. This may be seen by comparing fig. 15 *b* with fig. 17 *b*; in the latter section the proliferating mass on each side has divided, part being applied to the ventro-lateral corner of the ventral and part to the apposed corner of the dorsal sac (fig. 17 *b*, *Mes.*). The condition found in the posterior region of the last-described embryo (fig. 17 *c*) would be attained if the proliferating mass divided, only remaining connected by a layer of cells above, so that no septum would be present dividing the cavity of the embryo into two.

The main difference between this stage and the next may be best seen on examination of a section through the middle region of the ovum. In such a section (fig. 18 *b*) the two cavities, which were before only separated from one another by a single layer of protoplasm, are entirely distinct; each being bounded on all sides by a definite protoplasmic layer, and the walls, which are apposed to one another, being completely separated by a narrow space in which are found some of the small round elements, which are present in the space between the embryo and the vitelline membrane. Posteriorly the two sacs communicate as before (fig. 18 *c*); anteriorly the præoral lobes are very prominent (fig. 18 *a*, *p. o. l.*), there is a slight invagination of ectoderm (*St.*) in the middle ventral line, where the mouth will be found later, and there is a pair of definite hollow somites, which are the somites of the præoral lobes, lying one on each side of the yolk (fig. 18 *a*, *S. 1.*). The proliferations of nuclei which constitute the mesoblast are much larger and more clearly defined than in the last stage (*Mes.*) The peripheral yolk is entirely absorbed, but the whole embryo is still surrounded by the small round

elements, which are also very plentiful lying among the cells of the embryo, especially in the præoral lobes, and in the somites. These bodies, which are represented drawn under a high power in fig. 16, have a somewhat different form in this egg to that which they have in the previously described ones; they are still round in shape, but they contain in their interior a larger or smaller amount of vacuoles. The region in which the embryo is doubled on itself is shorter in this egg than in the preceding stage.

As was mentioned before the main difference between this and the previously described embryo is in the complete separation of the two sacs in that region where they are superposed upon one another. This change seems to have been effected by the ingrowth of the surrounding tissue, which by pushing in the septum causes it to become double. This process had already begun in the anterior region of the ovum of the previous stage, where in fig. 17 *a* the ventral sac is seen to be surrounded by a complete layer of ectoderm, while more posteriorly in the egg it is only separated from the dorsal sac by a single septum, as is shown in fig. 17 *b*.

In the next stage, sections of which are figured in figs. 19 *a—d*, the separation between the cavities has progressed still farther, the anterior tip of the ventral cavity, i. e. the posterior tip of the embryo, lying at some distance from the ventral wall of the dorsal one, as is shown in fig. 19 *b*. The region in which the embryo is doubled on itself is also shorter than before, so that it seems to be gradually straightening itself out. The embryo has also advanced considerably in other respects—the mouth is present as an ectodermic invagination (fig. 19 *b*, *M.*), the inner end of which forms the pharynx; the præoral lobes are united in front of the mouth by the cerebral commissure (fig. 19 *a*, *Cer. Com.*); the somites are present as a series of paired, hollow, thin-walled vesicles lying on the lateral faces of the body below the ectoderm, which in this region is slightly thickened. In the posterior portion of the body the somites are not yet present (fig. 19 *c*, *Mes.*), the mesoblast being still in the form of a pair of proliferating ridges of cells. The endoderm

is now for the first time clearly differentiated, and consists of a layer of nuclei surrounded by a very loosely reticulate layer of protoplasm, around the periphery of the inner yolk mass, and just within the ectoderm, except in the region of the somites, where it is subjacent to the splanchnic wall of the latter (figs. 19 *a—d*, *End.*). The small round bodies are still present, but in much smaller quantities than hitherto, both outside and among the cells of the embryo, from which fact it may be inferred that most of them have been absorbed; this reduction is shown in all the four figures (19 *a—d*).

In the next stage the straightening of the embryo within the shell had considerably progressed, the posterior end only being bent at an angle to the main part of the body. There is as yet no anus, so that the stomodæum is formed considerably earlier than the proctodæum. The somites are very distinct, with a thin splanchnic (fig. 20, *sp.*) and a thick somatic wall (fig. 20, *so.*); they do not contain in their cavities any of the small round elements found in them in previous stages. The ectoderm of the lateral body wall, i.e. that covering the somites, is thickened, and in the ventral regions of the thickening rounded elements are present, which will give rise to the future nerve-cords (fig. 20, *n. s.*). In the central yolk of this embryo (fig. 20) there are traces of the yolk segmentation, some of the segments containing nuclei; whether these traces have really been retained in this particular embryo longer than usual, or whether in the last few eggs which have been described they have been destroyed by the action of reagents is doubtful; the latter interpretation, however, seems possible, since in young segmenting embryos whose yolk could in the fresh state be very clearly seen to be segmented, the segmentation was only partially discernible in sections of them when preserved.

In all the eggs of stages subsequent to the segmentation which have been described hitherto, it was not possible to make out anything in a surface view of the embryo either in the fresh state or after preservation, owing to the peripheral yolk which surrounded it and completely obscured its external



characters. But in the next stage the peripheral layer has all become absorbed, and after the removal of the shell the features of the embryo can be clearly made out. Figs. 25 and 26, which represent an embryo of this stage seen from the side and front respectively, were drawn from an embryo after it had been preserved. The præoral lobes are very prominent, and are separated from one another ventrally by a rather shallow, wide median groove; the antennæ are beginning to bud out as small protuberances on their anterior dorsal corners. Along each side of the body is a longitudinal ridge, which is very clearly discernible by its prominence and also by its opaque white colour. This ridge is the origin of the appendages, and is anteriorly divided into distinct lobes, which are the rudiments of the appendages of the anterior segments of the body. The posterior end of the embryo is bent up almost at a right angle to the rest of the body, and at the tip where the lateral ridges meet there is a small papilla, which is perforated by the anus. The mouth is visible, situated on the ventral surface immediately behind the præoral lobes. Except on the præoral lobes, the lateral ridges, and the anal papilla, the body of the embryo is a dull yellowish colour, which is due to the yolk shining through the thin ectoderm.

In a series of transverse sections (figs. 21 *a*—*c*) through this embryo the following points are noticeable:

The ectoderm, except over the præoral lobes and the appendicular ridges, is a thin layer of flat cells. The cerebral lobes of the nervous system (fig. 21 *a*, *br.*) are connected in front of the mouth by a transverse commissure (fig. 21 *a*, *Cer. Com.*). The ventral cords are continuous with the brain, and form a pair of longitudinal ectodermic thickenings on the inner ventral angles of the leg ridges (figs. 21 *b* and 21 *c*, *n. s.*); they are not definitely separated from the ectoderm, but are distinguishable from it by the round elements of which they are composed. The mouth opens into a thick walled pharynx (fig. 21 *a*, *Ph.*), which is in communication with the gut. The anus is present (fig. 21 *c*, *an.*) on a terminal papilla, and is formed by a simple invagination of ectoderm. Immediately



behind the anus in the middle line there is a mass of undifferentiated cells (fig. 22, *pr. st.*), which is the primitive streak, a groove running down its centre being the primitive groove (fig. 22, *pr. gr.*). This is the earliest stage at which these structures are present, and the cells do not appear to be in a state of great activity.

The Mesoderm.—The somites are present as a series of paired hollow cavities on each side of the embryo. Their inner or splanchnic walls are very thin (figs. 21 *b* and 21 *c*, *Sp.*), but their outer are much thickened, and are composed of several layers of nuclei (figs. 21 *b* and 21 *c*, *So.*). In the anterior somites (fig. 21 *b*) the somatic wall has pushed out the thickened overlying ectoderm so as to form protuberances, which are the rudiments of the legs. A slight ventral outgrowth of the somatic wall towards the ectoderm is the rudiment of the duct of the segmental organ (fig. 21 *b*, *n. d.*). The posterior pair of somites communicate with one another across the middle line, and their posterior walls are fused with the undifferentiated tissues of the primitive streak.

The endoderm is present in the form of a layer of fairly regularly arranged nuclei lying in a protoplasmic reticulum round the periphery of the yolk (figs. 21 *a—c*, *End.*). There are a few nuclei in the central yolk, which latter is much less voluminous than in previous stages.

#### GENERAL CONSIDERATIONS.

The Segmentation.—So far as my material has allowed me to investigate the subject, the segmentation of *Peripatus novæ-zealandiæ* resembles closely that which has been described in some other Arthropoda. Quite lately Henking,<sup>1</sup> among others, has described the segmentation in the eggs of certain Phalangidæ, and his account in many respects agrees with that which I have given, noticeably in the formation of the blastoderm and in the irregular arrangement in the young stages of the nuclei composing it. The segmentation of the

<sup>1</sup> Henking, H., "Untersuchungen über die Entwicklung der Phalangiden," Theil i, 'Zeit. für wissen. Zool.,' xlv, 1886.

yolk, however, differs in that he considers each yolk-segment as a single cell, whereas in *P. novæ-zealandiæ* I find no relation existing between the yolk and the nuclei, it being quite a matter of chance whether or not a yolk-segment possesses a nucleus. Moreover, I do not think it necessary to suppose any free nuclear or cell formation to exist in the formation of the blastoderm, as there seems to be no reason why all the nuclei forming it should not be derived by division of the original segmentation nucleus. As to the nuclei which appear in the central part of the yolk, it is more difficult to account for them as originating from any pre-existing nucleus, as they are very far removed from any one, and the three chromatin particles in a mass of protoplasm, which are figured in fig. 10, rather point to the formation of nuclei by a process of aggregation of such particles. The segmentation also bears a considerable resemblance to that of *Peripatus capensis*; in fact the differences between the two may in all probability be accounted for by the presence of the yolk in the New Zealand species. They also resemble one another in the absence of any cell outlines, the protoplasm in *P. novæ-zealandiæ*, as in *P. capensis*, forming a perfectly continuous reticulum in which the nuclei are embedded; this is very especially noticeable in certain stages in the former species, as is shown in fig. 12. The curious forms assumed by the nuclei also resemble those found in *P. capensis*, although owing to the difficulty presented by the yolk in cutting sections of the young stages I was not able to get sections sufficiently thin to enable me to examine them in detail. It is nevertheless perfectly obvious that the nuclei often present the same curious phenomenon of being divided by septa into numerous compartments. These two points, however, viz. the continuity of the protoplasm and the forms of the nucleus, have been sufficiently discussed by Mr. Sedgwick in his papers on *P. capensis*, and need not be further considered here.

The mode of development from the segmentation up to the two last stages described in this paper presents many very curious facts, and indeed, so far as I know, is without any

exact parallel in the animal kingdom. It is particularly unfortunate that so many stages are wanting in my material, so that the exact sequence of events cannot be stated with any certainty. It seems strange that the early stages of all the three species of *Peripatus* should differ so remarkably from one another, while the later course of development seems to be nearly similar in all three.

It might be said of the mode of development of *P. novæ-zealandiæ* that the embryo is formed by a process of crystallising out in situ from a mass of yolk among which is a protoplasmic reticulum containing nuclei.

The two most remarkable features in the development are perhaps the mode of nutrition of the embryo and the mode of formation of the posterior part of the embryo, and it will be more convenient to discuss these two separately.

**Mode of Nutrition of the Embryo.**—As has been shown the embryo derives nutriment from two sources, (*a*) the yolk contained within its body; (*b*) a peripheral layer of yolk in which are embedded numerous small round, highly refractive bodies. The former of these sources need not be considered, as it is similar to that which occurs in many other eggs, which are loaded with food-yolk, being present in the hypoblast, but entirely absent in the mesoblast. It is with the peripheral yolk that we are concerned. The complete envelopment of the ovum in a thick peripheral layer of yolk is a very remarkable and unusual mode of embryonic nutrition, but its object evidently is to supply the ectoderm with a constant source of nourishment, the yolk first and the small round bodies eventually being completely absorbed by the ectoderm cells. It seems possible to regard it as ectodermal yolk, and it is very probably homologous with the peculiar arrangement in the ectoderm cells of *Peripatus capensis* which Mr. Sedgwick has described in the region of the hump. He says (These 'Studies,' pt. 1, vol. iv, p. 54,): "This increase in thickness" (i. e. of the ectoderm) "is mainly due to the appearance, outside the nuclei, of a layer of vacuolated protoplasm. The vacuolation . . . is a



very striking feature. The surface of the dorsal ectoderm, particularly of the hump, is very rough in these stages, and in the best preserved embryos without a definite external boundary. It presents very much the appearance which a bath-sponge would present in section, fraying out, as it were, into the surrounding fluid; and one may fairly conclude that during life it possesses the power of sending out processes into the fluid surrounding the embryo, and that the superficial vacuoles open to the exterior. In short, I am inclined to think that this surface ectoderm during stages E to F has a nutritive function, absorbing the fluid in which the embryo lies, and it seems to me conceivable that the placenta described by Kennel in the Trinidad species may be a more specialised organ of the same nature." It seems also conceivable that the peripheral layer of yolk in *P. novæ-zealandiæ* may be a more specialised organ of the same nature, and that originally when the ovum of *P. capensis* was provided with yolk, the space between the egg membrane and the ectoderm was filled with yolk, as is the case in *P. novæ-zealandiæ*, instead of as now with fluid. I have not been able to find processes on the external surface of the ectoderm cells, but the boundary is not very sharp, and the protoplasm passes without any definite limits into the peripheral layer. This is specially the case in the stages in which the internal yolk is divided by a longitudinal horizontal septum (vide fig. 17 *b* and 17 *c*). The modes of nutrition of Arthropod embryos are, as is well known, very variable, and an arrangement somewhat comparable to this is described by Ganin<sup>1</sup> as existing in *Platygaster*, where a layer of protoplasm containing nuclei surrounds the embryo, both the protoplasmic layer and the embryo being derived from precisely similar elements. He describes the first nucleus as arising as a new formation in the egg; from this another nucleus arises by division, and from this second one a third. The original nucleus gives rise by a process of complete segmentation to the embryo, the two later ones undergo division, and becoming sur-

<sup>1</sup> Ganin, M., "Beiträge zur Erkenntniss der Entwicklungsgeschichte bei den Insecten," 'Zeit. für wissen. Zool.,' xix, 1869.



rounded with protoplasm, arrange themselves as a layer round the embryo, in the formation of which they play no part. He does not say that this layer is used as food material, but considers it as a protective layer comparable in physiological significance to the amnion of an ordinary insect development. This process is very similar to that which occurs in *P. novæ-zealandiæ*, with the exception that the yolk is entirely wanting in the eggs of *Platygaster*. The peripheral yolk layer probably serves both as a nutritive and a protective layer, acting as a shield for the embryo in its young stages, since it does not become finally absorbed until the embryonic tissues have acquired considerable consistency, and so would no longer require such protection. Thus *P. novæ-zealandiæ* seems to have acquired by an extremely simple method an external layer which serves at once the double purpose of nourishing and protecting the embryo in its young stages.

A somewhat similar result is also brought about, although the means by which it is effected are quite different, in those insects which undergo an internal development, and in which the embryo is completely embedded in the yolk. The method of effecting this is considerably simpler in *P. novæ-zealandiæ* than in these insects, nothing corresponding to the amnion being present. It is possible that the amnion is a late development, acquired for the protection of the embryo, and that on its establishment it became involved with the external nutritive mass. However this may be, it is clear that there are various modes existing in Arthropods for the protection of the embryo and the nutrition of the ectoderm, and that these differ very largely in their mode of origin and in their structure, although they resemble one another in their physiological functions.

With regard to the small round bodies, which are so conspicuous a part of the peripheral layer, I have, as was said before, no definite knowledge as to their origin. From their form and structure one would be inclined to believe them to be derived from the yolk, but this is militated against by the fact that they stain a very deep red, whereas the yolk-spheres stain bright yellow, and it is difficult to imagine that some of the

yolk-spheres should suddenly change their properties towards staining reagents. The only other possible mode of origin for them is from the nuclei, which are present throughout the egg at the stage before these bodies are present. If this is the correct solution the nuclei must have been broken down and considerably altered before they were converted into their present form, since in the latter they are much smaller, instead of being granular they are homogeneous and highly refractive, and they stain much more deeply. Whatever their origin may be, they are undoubtedly an important factor in the nutrition of the egg, as they are found very plentifully scattered in the ectoderm in the comparatively early stages, and are afterwards absorbed without leaving a trace.

Mode of Formation of the Posterior End of the Embryo.—As was said in the descriptive part of this paper, I am unable to state with certainty the exact method by which the posterior end of the embryo is formed out of the egg; but however this may be effected, the condition attained in which the yolk contained in the anterior and posterior portions are separated only by a single thin layer of protoplasm is very remarkable, since at that stage the embryo possesses no definite ventral ectoderm, the ventral surfaces of the anterior or posterior halves being so closely applied to one another that the single protoplasmic septum belongs equally to each, and cannot be referred to one more than to the other.

In no other known type of development, so far as I know, does any process similar to this occur. It seems to have been acquired as a part of the peculiar crystallising-out process mentioned before as constituting one of the characteristic features in the development of this creature. It is no doubt a simple method for the formation *in situ* of the embryo, since it involves no doubling or growth in length within the egg; also, owing to the large space occupied by the peripheral nutritive layer, the amount of room within the egg is limited at this stage, and it would not be possible for the embryo to grow to any extent in length, so that the production of a doubled-up embryo *in situ* from a single embryonic mass

would doubtless be an easy and rapid mode of formation. It is not until after the peripheral nutriment has been mainly absorbed, so that the amount of space within the egg-shell is increased, that the posterior part of the body loses its close adherence to the anterior, and the embryo begins to straighten out. Also, apart from the space occupied by it, the peripheral yolk would probably act as a resistant force against a normal lengthways growth of the embryo. Ganin, in his account of the development of *Platygaster*, referred to above, describes a process whereby a result somewhat similar to that effected in *P. novæ-zealandiæ* is brought about:—the embryo after the segmentation is completed consists of a solid mass of cells, the peripheral layer being distinguished from the central mass by their more columnar form. An invagination of the ventral surface then occurs, forming a deep transverse fissure extending about half way across the embryo, and dividing it into an anterior cephalothoracic and a posterior caudal portion. So that at this stage the embryo has much the same characters as that of *P. novæ-zealandiæ* after the anterior and posterior regions of the body have acquired their own ventral walls and have become definitely distinct from one another. The stage in which the two are separated only by a single septum does not appear to possess any parallel in the development of *Platygaster*. But, apart from this, the formation in situ of an embryo doubled upon itself from a primitively single and solid mass is very remarkably similar in the two cases. It would appear to have been acquired as a simple process, the conditions being, in the fact of the enclosure of the embryo in a peripheral layer, somewhat similar in both ova.

Origin of the Endoderm.—As I said in my remarks on the segmentation, the first endodermal nuclei seem to arise by a process of free nuclear formation. The same may perhaps be the case with the later endodermal nuclei, since in no case have I found any trace in them of karyokinetic figures, which latter are extremely common in all the other nuclei. At the stage before the embryo is definitely formed, when the flattened protoplasmic plate is present along one side of the egg, there



are a few nuclei present in the central yolk, and these probably are the early endodermal nuclei. At the stage when the embryo is first definitely formed, and lies as a sac within the peripheral layer, there are nuclei present within the body of the embryo; these are irregular angular bodies with a granular structure, scattered irregularly in the central yolk, often containing one or two chromatin particles; their boundary is often indistinct, so that the nuclear passes imperceptibly into the protoplasmic substance. Later, the endoderm nuclei are much more numerous, and are arranged round the periphery of the yolk in a regular manner. Since in no case whatever at any stage have I found the least trace of any karyokinetic figures in these endodermic nuclei, and as also I often find in the central yolk all stages, from small masses of chromatin up to definite, large, fully-formed nuclei, I am inclined to believe that they arise by a process of free nuclear formation, and that no nuclear division takes place, at all events, till after the stage at which the endoderm is present as a definite layer at the periphery of the central yolk mass.

#### SUMMARY.

1. The ripe ovum of *P. novæ-zealandiæ* is very heavily charged with food-yolk, which causes it to be of comparatively large size.

2. The segmentation is on the centrolecithal type; the protoplasm is mainly at one pole of the egg, and in this protoplasm nuclei arise, probably by the division of the original segmentation nucleus. The protoplasm forms a loose reticulum containing nuclei on the surface of the egg, which first extends over only a small area, but later spreads over the surface, until in the latest stage which I have, it covers about half the periphery of the egg.

3. In the latest segmenting ova there are small masses of protoplasm in the centre of the egg; occasionally one of these may contain a nucleus, and in one case three chromatin masses are present in one of these protoplasmic areas.

4. Shortly after the segmentation begins the yolk becomes



divided up into a number of rounded segments, which, however, bear no relation to the true segmentation.

5. The protoplasm is in the form of a reticulum, and there are no traces of cell outlines.

6. In the next stage, which I have examined after the segmentation, there is a specially marked area of reticulate protoplasm, containing a large number of nuclei extending through about one third of the length of the ovum, and having in transverse section an irregular triangular shape, the base of the triangle resting on the surface of the egg. Nuclei are present throughout the whole of the yolk, being more numerous at the periphery than at the centre.

7. The triangular-shaped protoplasmic area becomes more compact and flattens itself out, forming a plate-like mass of protoplasm densely packed with nuclei on the surface of the egg. Its lateral edges turn slightly inwards away from the periphery. The nuclei over the rest of the egg have undergone no change.

8. The embryo is present as a closed sac, the walls of which are separated from the vitelline membrane by a thick layer of yolk, in which small round, highly refractive bodies are present. The embryo is enclosed in a thin layer of protoplasm, with nuclei, which represents the ectoderm. Along one line, in a longitudinal direction, there is a prominent ridge on the outer side of the ectoderm, composed of proliferating nuclei. Anteriorly this ridge divides into two, which remain attached to one another above and below, in such a way as to enclose a cavity between them.

9. At the next stage the rudiments of the præoral lobes are present in the form of a thickened mass of cells at the ventro-lateral corners of the embryo. At a very short distance from the anterior end of the embryo the yolk is divided by a protoplasmic septum, which runs in a longitudinal horizontal direction, and separates the body of the embryo into two sacs, one lying above the other. The septum stops short at a short distance from the posterior end, so that the two sacs communicate freely round its end. At the regions where the septum joins the body

wall on each side of both sacs there is a thickening of the cells, which is the rudiment of the mesoderm. The peripheral yolk is mostly absorbed, but the small round bodies are still present in large quantities as before, outside the embryo, and among its cells.

10. The septum has become divided into two layers by a process of ingrowth of the surrounding tissue, so that each sac is completely enclosed by a protoplasmic layer, and the embryo now consists of a sac doubled on itself in such a way that the ventral face of the anterior part of the body is opposed to that of the posterior part of the body. Indications of cavities have appeared in the mesoblastic bands, which are the rudiments of the somites.

11. The embryo begins to straighten itself out, the ventral surface of the posterior end gradually removing itself farther from that of the anterior. The mouth is present as an invagination of ectoderm on the ventral surface just behind the præoral lobes. The endoderm is present as a layer of nuclei surrounded by a reticulum of protoplasm lying at the periphery of the yolk. The somites are present in the anterior region in the form of a series of definite cavities at the sides of the body. The small round bodies outside the body of the embryo are almost entirely absorbed.

12. The embryo is still further straightened out, so that the only indication of the doubling is in the fact that the posterior end of the body is bent up at an angle to the anterior. The anus is not yet formed. The somites are present throughout the whole length of the embryo, and in the anterior ones the somatic wall is thicker than the splanchnic.

13. The peripheral food material is completely absorbed, so that the embryo lies just within the vitelline membrane and egg-shell. The appendages begin to appear as blunt rounded protuberances on a lateral ridge which runs along each side of the body. The antennæ arise as buds on the præoral lobes. The anus is present, situated on a papilla at the posterior end of the body, and consisting of a simple ectodermic invagination. A primitive streak and groove are present, anterior to and on

the dorsal side of the anus. The central yolk mass is much reduced in bulk. The somatic wall of the somites is much thickened, and in the anterior segments pushes out the ectoderm covering it, so as to form the leg portion of the somite; a small ventral outgrowth represents the rudiment of the nephridial duct. The ectoderm over the leg ridges is thickened, and at the internal ventral angles of this thickening there are special rounded elements which are the origin of the nerve-cords. The cerebral lobes of the nervous system are joined together in front of the mouth by a cerebral commissure.

In conclusion, I wish to express my thanks to Mr. Sedgwick for his kindness in providing me with my material, and for the assistance which he has given me throughout my work.

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## EXPLANATION OF PLATES XXII, XXIII, XXIV, XXV and XXVI,

Illustrating Lilian Sheldon's paper "On the Development of  
*Peripatus novæ-zealandiæ*."

### *List of Reference Letters.*

*an.* Anus. *Ap.* Appendage. *At.* Antenna. *br.* Brain. *Cer. Com.* Cerebral commissure. *Ch.* Chorion. *Ec.* Ectoderm. *End.* Endoderm. *L. S.* Leg portion of somite. *M.* Mouth. *Mes.* Mesoblast. *n.* Nucleus. *n. d.* Nephridial duct. *n. s.* Nerve cord. *Ph.* Pharynx. *Pm.* Protoplasm surrounding nucleus. *Pm. A.* Protoplasmic area. *Pm. S.* Protoplasmic segments. *p.* Cavity in proliferating mass of nuclei. *p. n.* Proliferating mass of nuclei. *p. o. l.* Præoral lobe. *post. Em.* Posterior end of embryo. *pr. g.* Primitive groove. *pr. st.* Primitive streak. *p. y.* Peripheral yolk. *S.* Somite. *Sep.* Septum between the two cavities. *So.* Somatic wall of somite. *Sp.* Splanchnic wall of somite. *St.* Stomodæal invagination. *V. m.* Vitelline membrane. *Y.* Yolk in the embryo. *Y. S.* Yolk segments.

All the figures, except Nos. 23, 24, 25 and 26, were drawn with Zeiss's camera lucida; the power under which it was drawn is stated after the description of each figure.

FIG. 1.—Transverse section through an unsegmented ovum, in which the nucleus is at some little distance from the periphery. The yolk is unsegmented. *n.* Nucleus. *Y.* Yolk. *Pm.* Protoplasm surrounding the nucleus. Oc. 2, obj. B.

FIG. 2.—Section through a small portion of an unsegmented ovum, showing the nucleus situated close to the periphery. *n.* Nucleus. *Pm.* Protoplasm surrounding the nucleus. *Y.* Yolk. *V. m.* Vitelline membrane. *Ch.* Chorion. Oc. 2, obj. D.

FIGS. 3*a* and 3*b*.—Transverse sections through an ovum, in which two nuclei are present, and in which the yolk has not begun to segment.

Fig. 3*a* passes through one nucleus, which is situated at the periphery of the egg, and has a lobed form.

Fig. 3*b* passes through the other nucleus, which is at the same pole as that in Fig. 3*a*, but lies deeper in the egg. It is in a state of division, the section passing transversely through the spindle. *n.* Nucleus. *Pm.* Protoplasm surrounding the nucleus. *Y.* Yolk. Oc. 2, obj. B.



FIGS. 4*a-c*.—Three transverse sections through an ovum containing three nuclei, and in which the yolk has begun to segment.

FIG. 4*a* shows the whole egg. At one pole a round nucleus is present, and the yolk has begun to segment, the yolk-spheres at that pole being smaller than over the rest of the egg. Oc. 2, obj. CC.

FIG. 4*b* shows only the pole of the egg containing the second nucleus and the yolk segmentation. The nucleus is much lobed. Oc. 2, obj. D.

FIG. 4*c* passes through the third nucleus, and shows only a small portion of the egg. The nucleus is lobed and very irregular in shape. *n*. Nucleus. *Pm*. Protoplasm surrounding the nucleus. *Y*. Yolk. *Y.S*. Yolk segments. Oc. 2, obj. D.

FIG. 5.—Transverse section through the protoplasmic pole of the ovum, which is shown in surface view in Fig. 24. The protoplasm is seen to consist of a reticulum, in which the nuclei lie irregularly. *n*. Nuclei. *Pm*. Protoplasm. *Y.S*. Yolk segments. Oc. 2, obj. CC.

FIG. 6. Section through a small portion of the protoplasmic pole of the same egg as Fig. 5, highly magnified, to show the irregular arrangement of the nuclei, twelve of them being closely packed together in a small reticulate area of protoplasm. Oc. 4, obj. E.

FIG. 7*a*.—Transverse section through the protoplasmic pole of an ovum, slightly older than that from which Figs. 5 and 6 were drawn, showing how the protoplasm has spread over a larger portion of the surface of the egg; it still forms a perfectly continuous reticulum. Oc. 2, obj. D.

FIG. 7*b*.—Section through the same ovum near the limit of the protoplasmic area, to show how the protoplasmic areas are connected together by strands. Oc. 2, obj. D.

FIG. 8.—Transverse section through the protoplasmic pole of an ovum, in which the protoplasm extends over a larger area of the surface of the egg than it did in the preceding figures. The protoplasmic segments are rather more distinct from one another than they were in the preceding figures, but are still connected by strands. *Pm.S*. Protoplasm segments. *Y.S*. Yolk segments. *V.m*. Vitelline membrane. *n*. Nuclei. Oc. 2, obj. D.

FIG. 9.—Section through half of an egg of about the same stage as that shown in Fig. 8, in which the protoplasmic segments are more distinct from one another than is usually the case. *n*. Nuclei. *Pm.S*. Protoplasmic segments. *Y.S*. Yolk segments. *V.m*. Vitelline membrane. Oc. 2, obj. CC.

FIG. 10.—Transverse section through an egg, in which the protoplasmic segments have extended fully half-way round the periphery. The protoplasmic areas are separated from one another by considerable tracts of yolk; one area lies quite at the surface, and contains a large round nucleus which appears to be about to divide. Three protoplasmic masses are present in the central yolk, one of which contains three chromatin particles. The yolk does not

appear to be segmented, but this may be due to the action of reagents. This figure was compounded from two sections. *Pm. S.* Protoplasmic segments. *Y.* Yolk. *n.* Nuclei. Oc. 2, obj. CC.

FIG. 11.—Transverse section through the middle of an ovum, in which there is a special area of protoplasm at one pole forming a reticulum, in which many nuclei lie. Nuclei are also present scattered through the yolk. The yolk is segmented. *Pm. A.* Protoplasmic area. *Y. S.* Yolk segments. Oc. 2, obj. A.

FIG. 12.—The protoplasmic area of the ovum shown in Fig. 11, more highly magnified, to show the reticulate arrangement of the protoplasm, the absence of cell outlines, and the irregular arrangement of the nuclei. Oc. 2, obj. D.

FIG. 13.—Transverse section of an ovum, rather older than that from which Fig. 11 was drawn. The protoplasmic area (*Pm. A.*) has become more compact and flattened. The nuclei in the rest of the egg are more numerous round the periphery than in the centre. The ovum is broken at two points. *Pm. A.* Protoplasmic area. *V. m.* Vitelline membrane. Oc. 2, obj. A.

FIG. 14.—The protoplasmic area shown in Fig. 13, more highly magnified, to show the absence of cell outlines. Oc. 2, obj. D.

FIGS. 15*a-d*.—Four transverse sections through the youngest ovum, in which the embryo is definitely formed. *Ec.* Ectoderm. *p.* Cavity in the proliferating mass of nuclei. *p. n.* Proliferating mass of nuclei. *p. y.* Peripheral layer of yolk. *V. m.* Vitelline membrane. *Y.* Yolk within the embryo. Oc. 4, obj. A.

Fig. 15*a*. Section through the anterior end of the ovum, in front of the embryonic region, showing the segmented condition of the peripheral yolk in this region.

Fig. 15*b*. Section through the anterior part of the embryonic region, showing the embryo surrounded by the peripheral yolk layer.

Fig. 15*c*. Section through the middle of the embryonic region, showing the embryo surrounded by the peripheral yolk and enclosed in the ectoderm, on one point of which is the proliferating mass of nuclei. The small round bodies are shaded very dark.

Fig. 15*d*. Section through the posterior end of the embryo, shortly anterior to its termination and behind the region of the proliferating ridge.

FIG. 16.—Shows a group of the small round bodies of the peripheral yolk layer from the embryo shown in Figs. 18*a-c*, highly magnified. They are vacuolated. Reichert's  $\frac{1}{15}$  oil immersion.

FIGS. 17*a-c*.—Three sections through an embryo, somewhat older than that from which Figs. 15*a-d* were drawn. *Ec.* Ectoderm. *Mes.* Mesoblast. *p. o. l.* Præoral lobes. *post. Em.* Posterior tip of the embryo. *Sep.* Septum. *V. m.* Vitelline membrane. Oc. 4, obj. A.

Fig. 17*a* is a somewhat oblique section through the anterior end of the ovum. It passes through the posterior tip of the embryo (*post. Em.*), which is distinct from the ventral wall of the anterior end, being surrounded by a complete layer of ectoderm. Owing to the obliquity of the section the right præoral lobe is considerably larger than the left.

Fig. 17*b* is through the middle of the ovum, where the anterior and posterior ventral surfaces of the embryo are only separated from one another by a single protoplasmic septum (*Sep.*)

Fig. 17*c* is through the hind part of the egg, behind the region of the septum, where the anterior and posterior portions of the embryo are in free communication with one another.

FIGS. 18*a—c.*—Three transverse sections through an ovum, rather older than that figured in Figs. 17*a—c.* *Ec.* Ectoderm. *Mes.* Mesoblast. *p. o. l.* Præoral lobes. *p. y.* Remains of peripheral yolk. *S.* Somites. *St.* Stomodæal invagination. *V. m.* Vitelline membrane. *Y.* Yolk. Oc. 3, obj. A.

Fig. 18*a* passes through the anterior end of the embryo, in the region of the præoral lobes. The ectoderm has begun to invaginate in the middle ventral line to form the stomodæum, and the somites of the præoral lobe segment are present (*S. 1.*). The space between the embryo and the vitelline membrane is occupied by a large number of the small round bodies, which are also present among the tissues of the embryo.

Fig. 18*b* passes through the middle of the ovum. The ventral surfaces of the anterior and posterior regions of the body are completely separate from one another. The somites of the trunk are beginning to appear (*S.*)

Fig. 18*c* passes through the hind of the embryo, where the anterior and posterior portions of the embryo are continuous.

FIGS. 19*a—d.*—Four rather oblique transverse sections through an ovum, in which the embryo is still doubled on itself, though rather less so than in the ovum from which Figs. 18*a—c* were taken, and the space between the apposed ventral surfaces is greater. In this ovum the endoderm is first definitely differentiated as a distinct layer. A few small round bodies are still present between the vitelline membrane and the ectoderm, but most of them have by this time been absorbed. *Cer. Com.* Cerebral commissure. *Ec.* Ectoderm. *End.* Endoderm. *M.* Mouth. *Mes.* Mesoderm. *p. o. l.* Præoral lobes. *post. Em.* Posterior tip of the embryo. *S.* Somite. *V. m.* Vitelline membrane. Oc. 3, obj. A.

Fig. 19*a* passes through the anterior end of the embryo in front of the mouth, in the region of the cerebral commissure.

Fig. 19*b* passes through the mouth of the embryo. The posterior tip is shown lying on the ventral side of the ovum, separated by a considerable space from the mouth.

Fig. 19*c* is from a section posterior to the above. It passes through the anterior part of the embryo behind the mouth, on one side passing



through the posterior end of the præoral lobe; and through the posterior part of the embryo in the region behind that where the somites are present, the mesoblast (*Mes.*) being solid.

Fig. 19*d* passes through the posterior end of the ovum, in the region where the anterior and posterior portions of the embryo are continuous with one another.

FIG. 20.—Transverse section through an embryo which has become almost completely straightened out. The somatic wall (*So.*) of the somites is thickened, as also is the ectoderm lying over it. *End.* Endoderm. *n. s.* Rudiments of ventral nerve-cords. *S.* Somite. *Sp.* Splanchnic wall of somite. *So.* Somatic wall of somite. Oc. 4, obj. A.

FIGS. 21*a-c*.—Three transverse sections through the embryo, which is shown in surface view in Figs. 25 and 26. *an.* Anus. *Cer. Com.* Cerebral commissure. *End.* Endoderm. *br.* Brain. *L. S.* Leg portion of the somite. *n. d.* Rudiment of nephridial duct. *n. s.* Ventral nerve-cord. *Ph.* Pharynx. *S.* Somite. *Sp.* Splanchnic wall of somite. *So.* Somatic wall of somite. Oc. 4, obj. A.

Fig. 21*a* is taken just in front of the mouth, in the region of the cerebral commissure. The pharynx is seen in communication with the gut.

Fig. 21*b* passes through the appendage of the left side, and shows the somite dividing into a leg and a body portion, and also the ventral outgrowth which will form the nephridial duct.

Fig. 21*c* passes through the anus, and the lateral ridge behind the region, where it is divided into appendages.

FIG. 22.—Shows the primitive streak, and is taken from a section a little posterior to that shown in Fig. 21*c*, but it is more highly magnified. *End.* Endoderm. *pr. g.* Primitive groove. *pr. st.* Primitive streak. Oc. 2, obj. D.

FIG. 23.—Surface view of a segmenting ovum, to show the yolk segmentation. *Ch.* Chorion. *Y. S.* Yolk segments.

FIG. 24.—Surface view of a segmenting ovum. The protoplasmic segments are seen lying on the surface of the egg. The yolk segmentation is not seen, owing to the surface of the egg having been slightly disintegrated by the preserving reagents. The chorion and vitelline membrane have been removed.

FIG. 25.—An embryo, in which all the peripheral nutritive layer has been absorbed, viewed from the side; showing the large præoral lobe with the antenna budding out from it, and the lateral ridge with five distinctly formed appendages (*Ap.*).

FIG. 26.—The same embryo seen from the ventral side, and showing the mouth and anus and primitive groove, in addition to the structures seen in the last figure. These two drawings were from an embryo preserved in picric acid. *an.* Anus. *Ap.* Appendages. *At.* Antennæ. *M.* Mouth. *p. o. l.* Præoral lobe. *pr. gr.* Primitive groove.







Fig. 1.

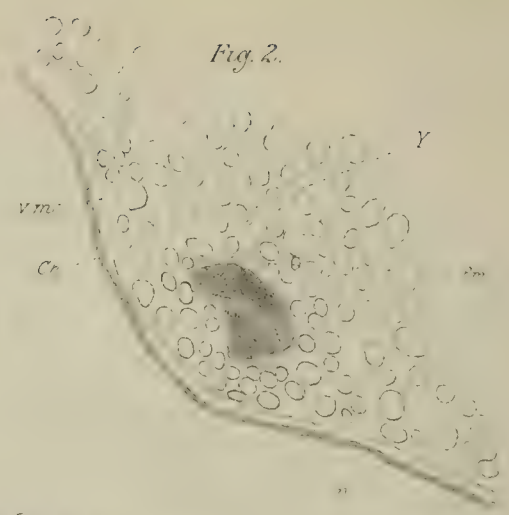


Fig. 2.

Fig. 3a.

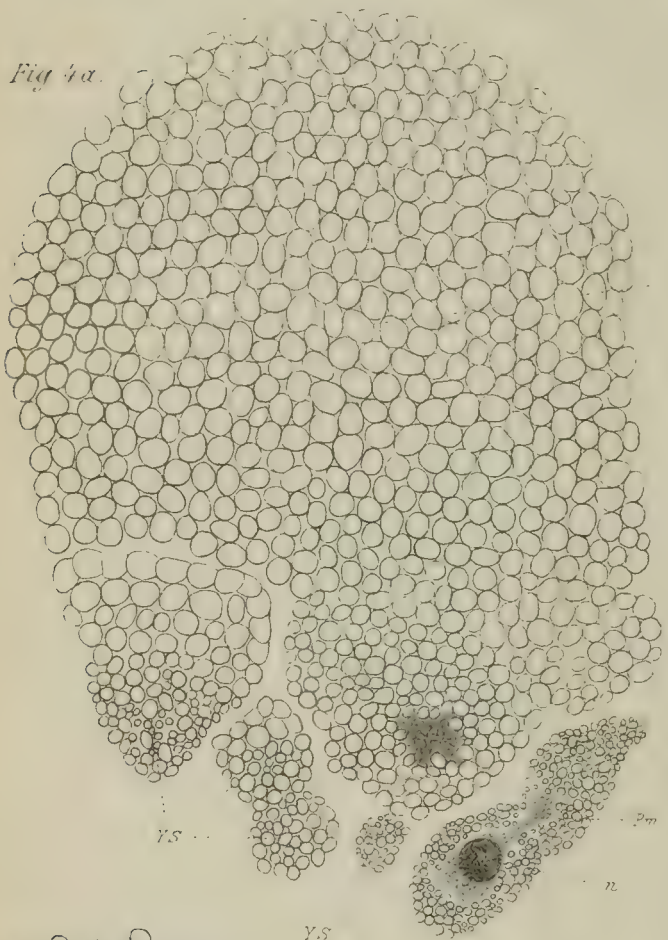
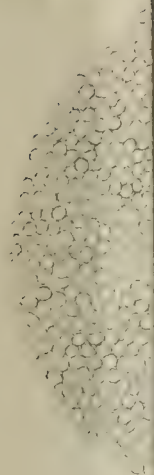


Fig. 4a.

Fig. 4b.

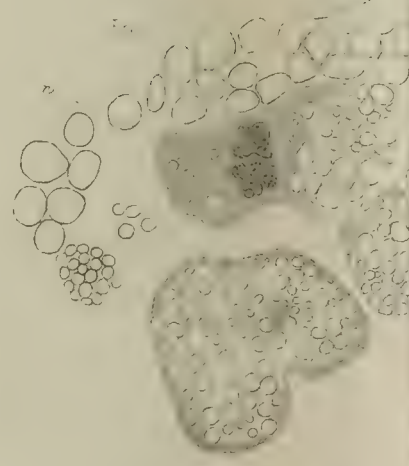


Fig. 4c.

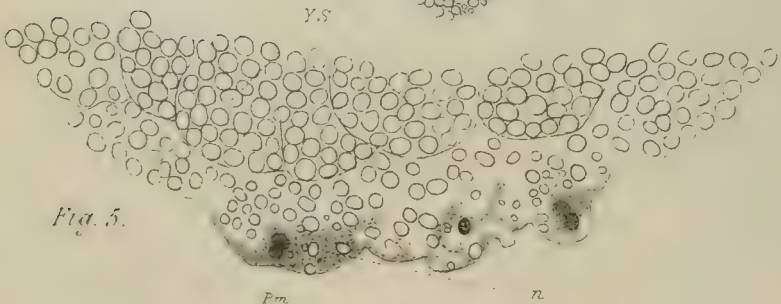
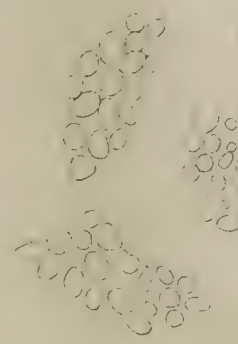
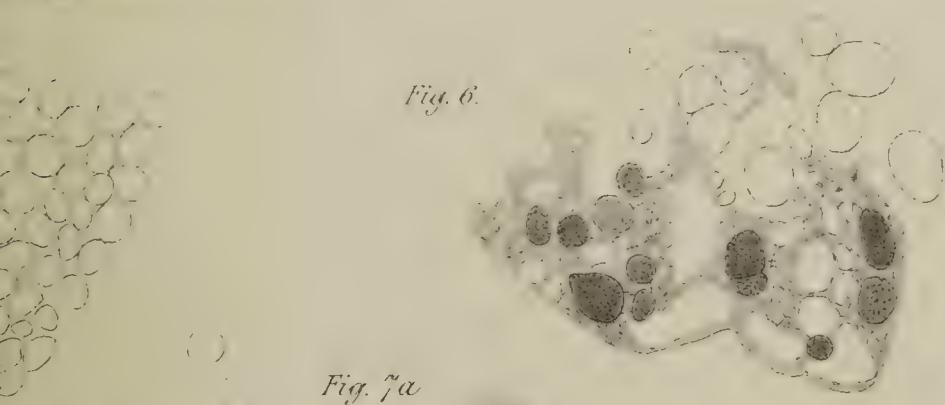


Fig. 5.

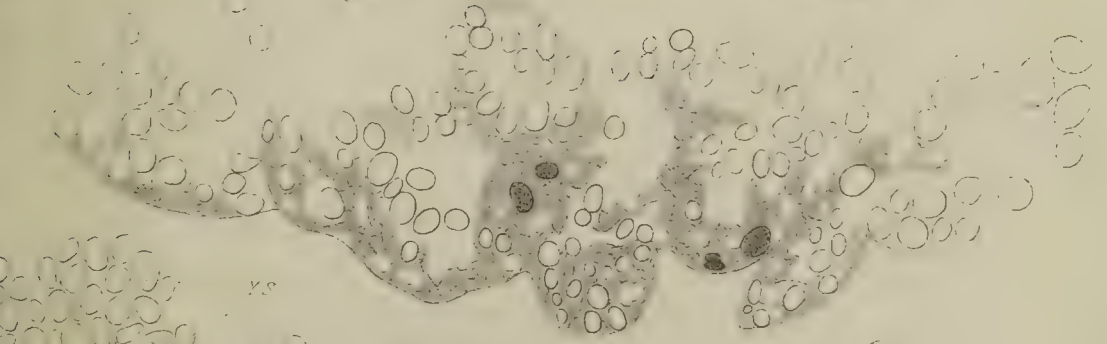
*Fig. 3b*



*Fig. 6.*



*Fig. 7a*



*Fig. 7b*

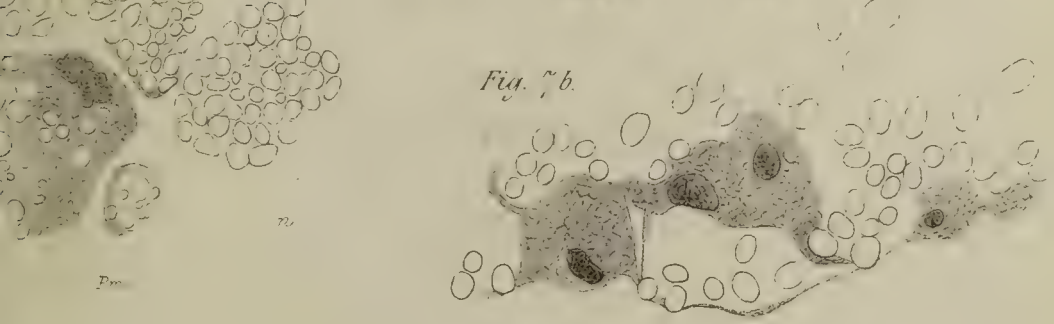








Fig. 8.

Y.S.

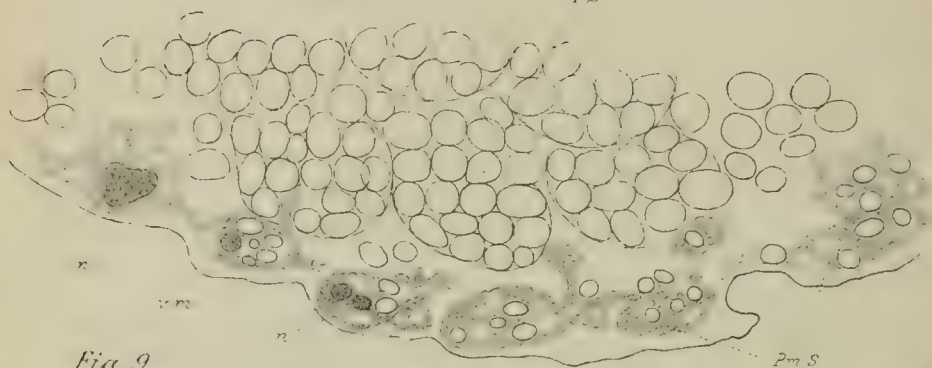


Fig. 9.



Fig. 10.

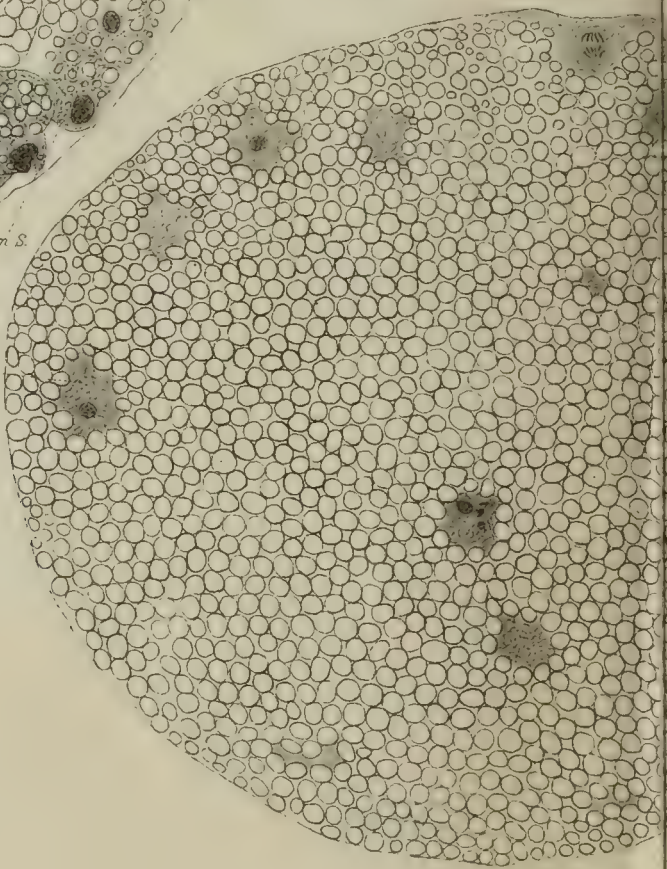


Fig. 13.



Fig. 12.

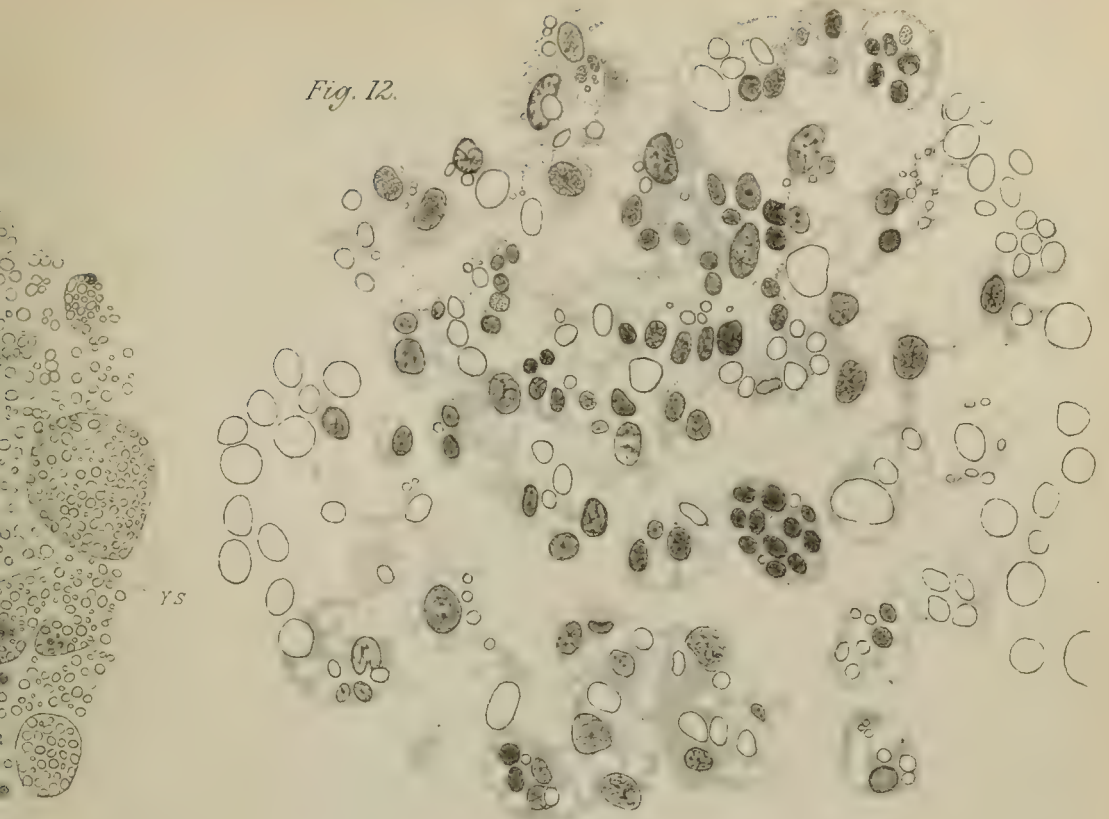


Fig. 14.

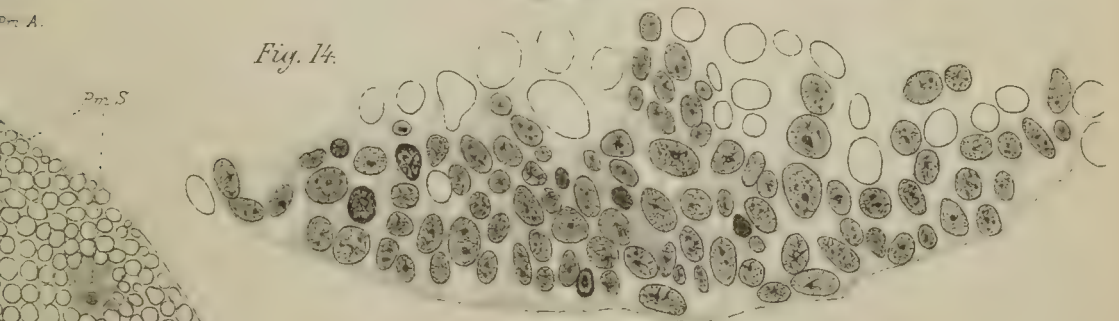
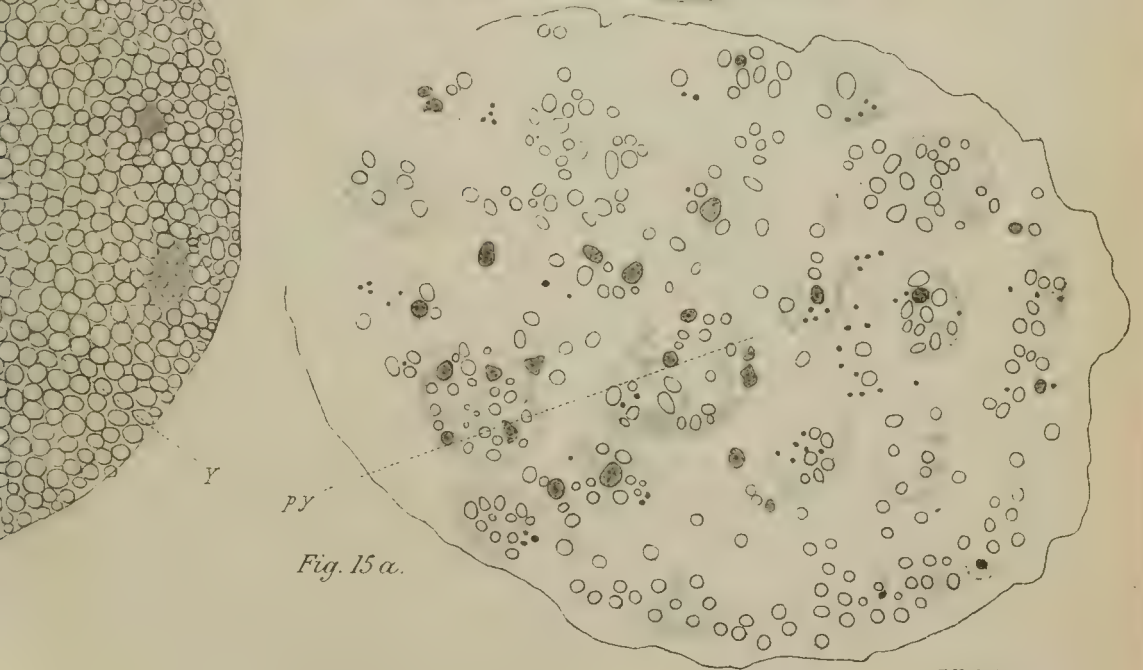


Fig. 15 a.







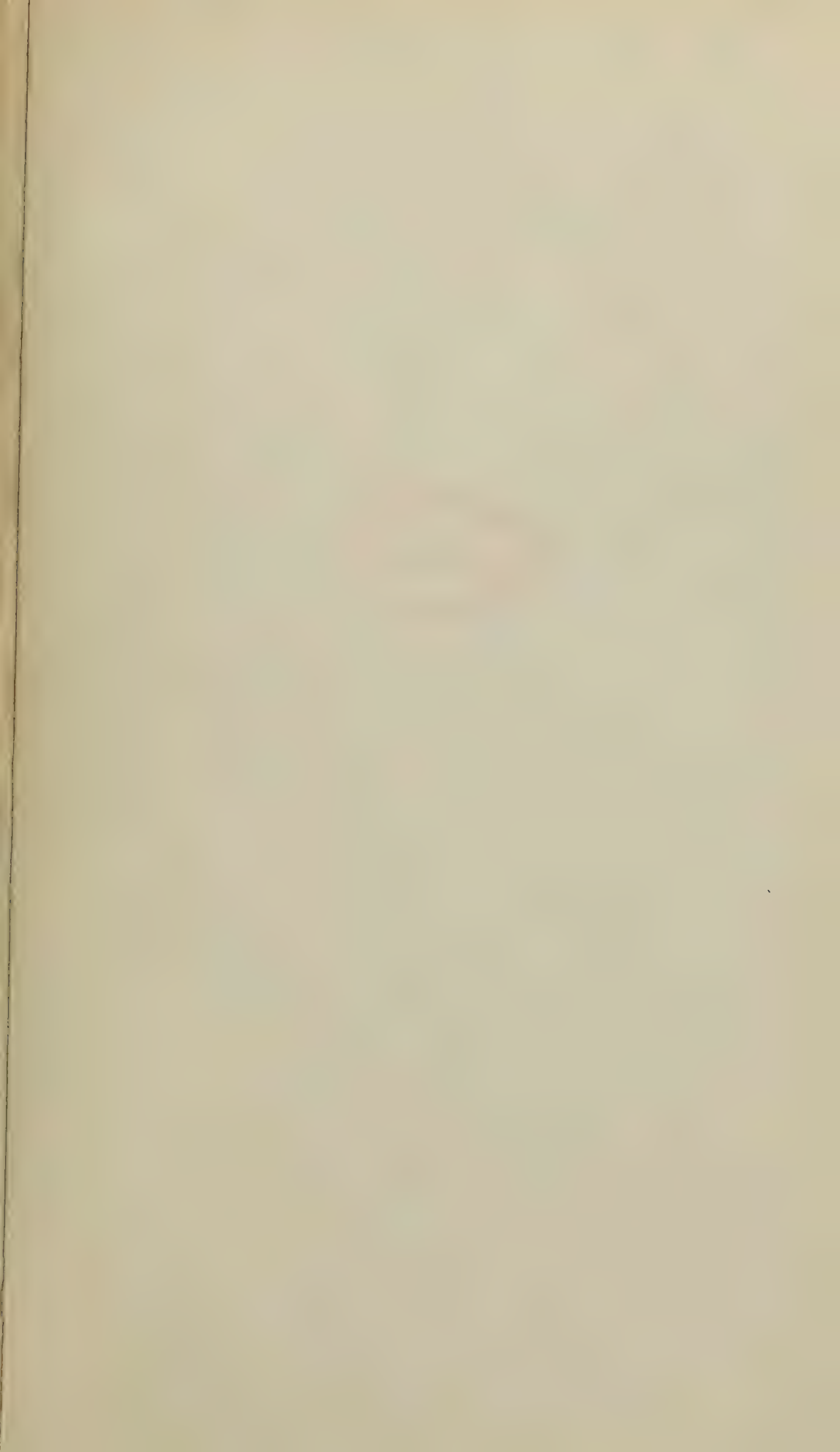


Fig. 15b.



Fig. 15c.

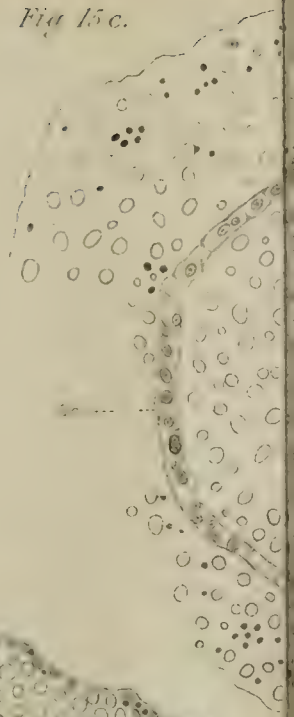


Fig. 17b.

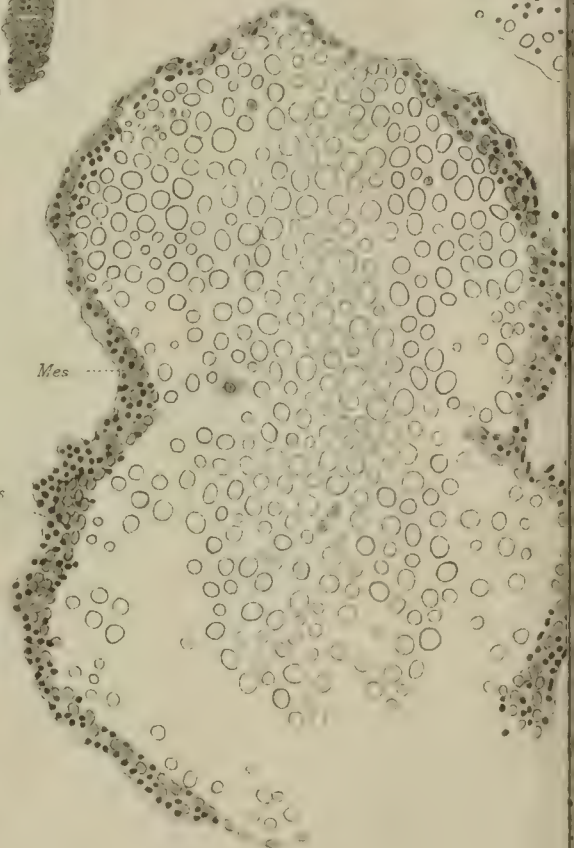


Fig. 17c.

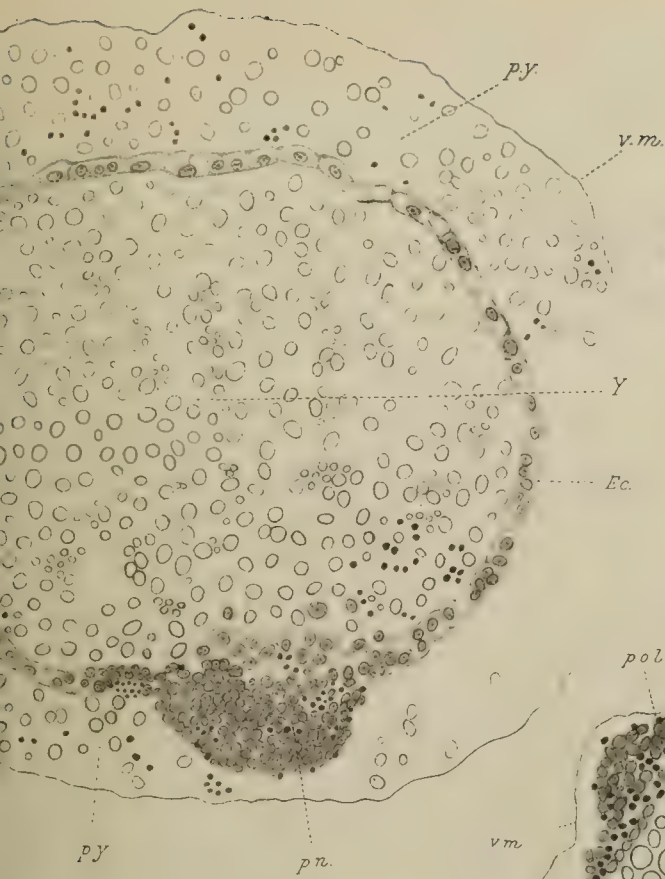


Fig. 15 d.

Mes

Mes.

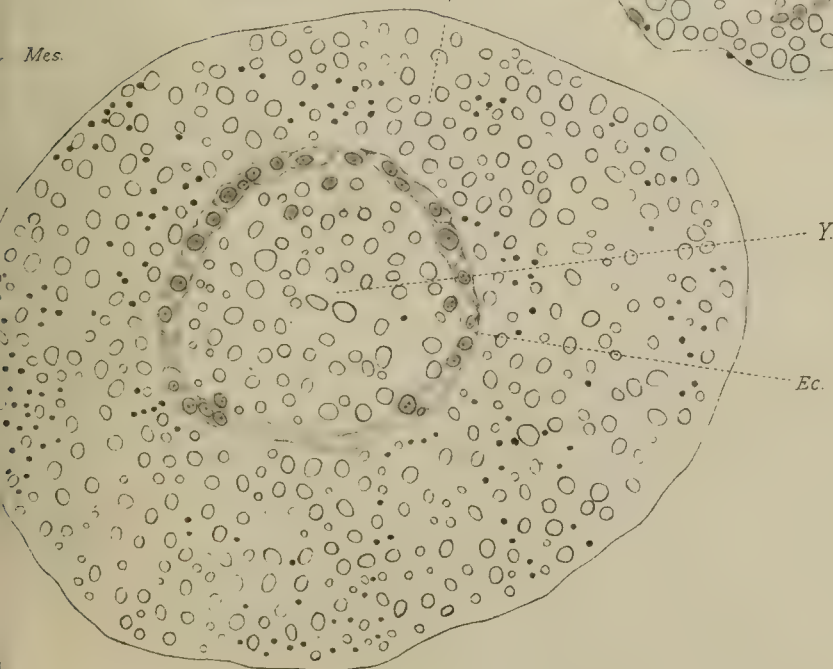


Fig. 16.









Fig. 18 a



Fig. 18 b

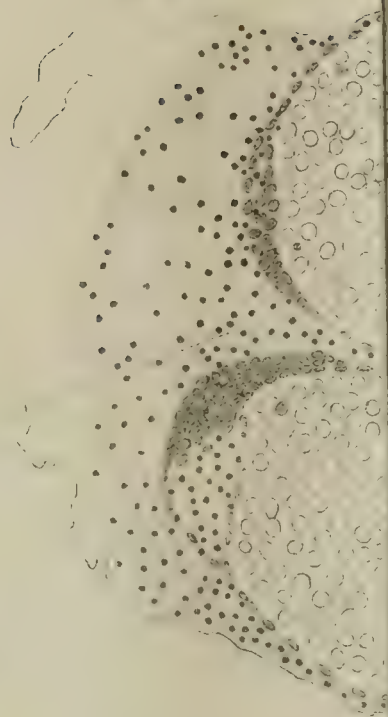
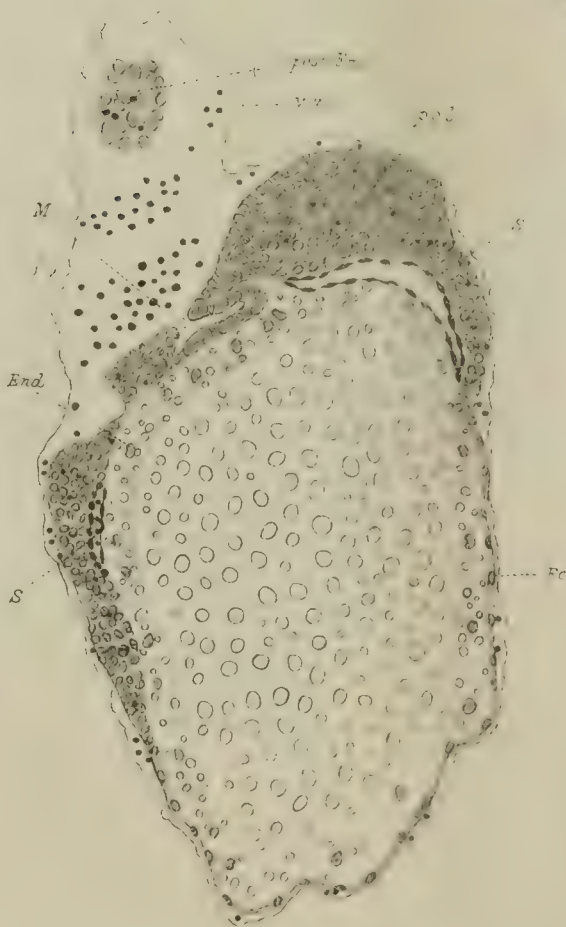


Fig. 19 a



Fig. 19 b



Es

Fig. 18 c.



Fig. 19 d.









Fig. 21a

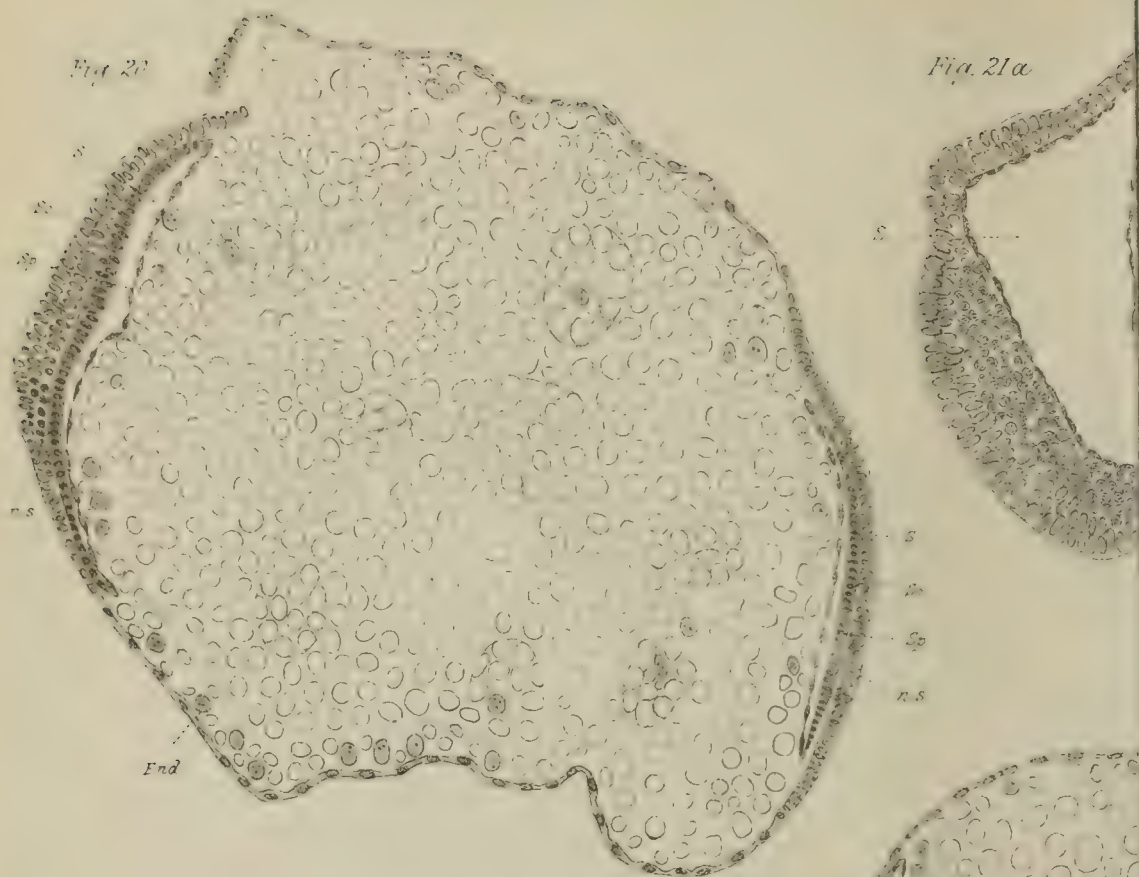


Fig. 21b.



Fig. 21c.



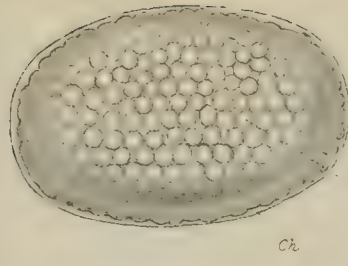
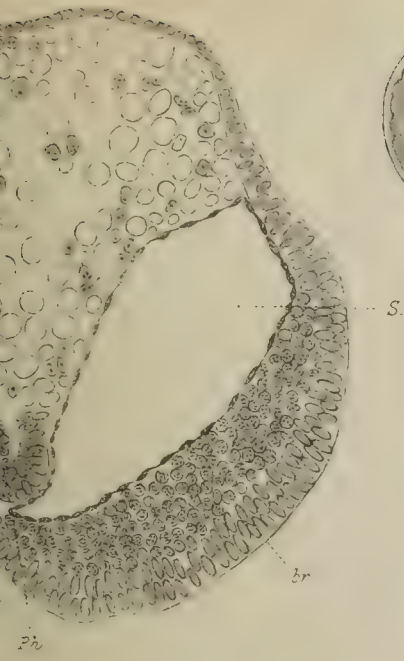


Fig. 23.

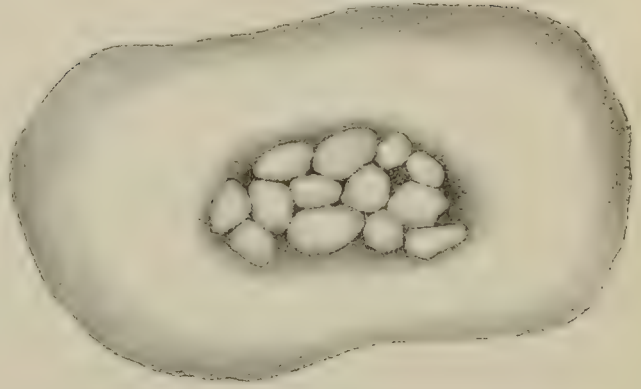


Fig. 24



Fig. 22.



Fig. 26.

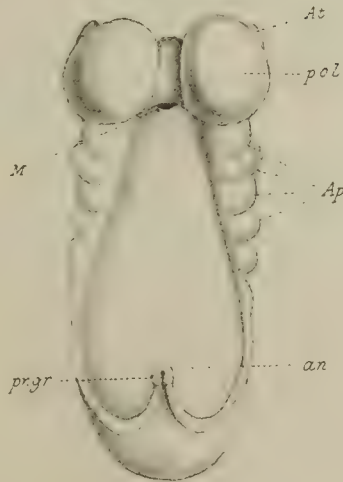
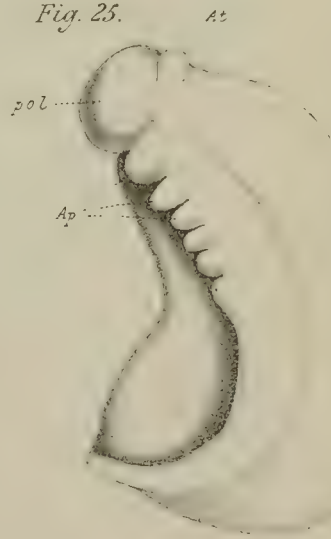


Fig. 25.







## On the Development of Peripatus Novæ-Zealandiæ.

By

**Lillian Sheldon,**

Bathurst Student, Newnham College, Cambridge.

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With Plates XXVII and XXVIII.

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IN January last, through the kindness of Mr. Sedgwick, I received another supply of *Peripatus novæ-zealandiæ*.

As before, they arrived in the living condition, and the eggs were removed from the uterus immediately after the animal had been killed with chloroform.

The proportion of males was considerably larger than on previous occasions, being twenty-two out of a total of forty-nine. There were nine smallish females which contained no embryos; and in the remainder, which varied in size from about three-quarters to two inches in length, the uteri were filled with embryos. The number of embryos in a single female varied considerably, the maximum being eighteen and the minimum seven.

Most of the embryos were preserved in corrosive sublimate and glacial acetic acid used hot, but the best results were obtained from some which were placed for six or seven hours in a mixture consisting of equal parts of .5 per cent. chromic acid and 2 per cent. acetic, and afterwards washed in alcohol. In this method it is not necessary to prick the egg-shell before the embryo is removed to alcohol. After this method of preservation, which is that recommended by Hertwig for amphibian

eggs, the yolk is rendered much less brittle than after any other methods which I have tried; the protoplasm and nuclei are well preserved, and also the egg-shell expands and lies at some distance from the periphery of the ovum, and so can easily be removed. The eggs were all stained with picro-carmin, and passed through the various strengths of alcohol in which a small quantity of picric acid was dissolved.

The embryos, with the exception of a few quite old ones, were all of stages between those shown in figs. 10 and 15 in my last paper (3), that is, they came in age between those received in December and April respectively.

My material is again very incomplete, and the new stages which I shall describe, though they throw some light on the early development, are very few, and do not unfortunately by any means fill up the gaps which were left in the account of the development given in my last paper (3); but it seemed advisable to publish my results, in the hope that they might prove useful if anyone should have the opportunity of working on the development of this interesting species with a better supply of material than I have been able to obtain.

The ovum, which represented the latest segmentation stage, described and figured (fig. 10) in my last paper (3), was one which was taken out of the uterus in December. In it the nuclei were present round slightly more than half the ovum, lying in small masses of branched protoplasm. The central one of these nuclei lay on the surface and showed signs of karyokinetic figures. There were also two or three protoplasmic masses in the central yolk. I have now (in the January lot) several stages later than this, which show that the nuclei in the centre of the surface of the ovum beneath which they lie multiply with considerable speed and very much more quickly than those over the rest of the ovum, a condition which is shown in fig. 4, until by their repeated increase the egg acquires the form shown in fig. 11 (3), which represented a transverse section through an April ovum. In the ovum there figured there is a specially-marked area of reticulate protoplasm, containing a large number of nuclei extending through

about one third of the length of the ovum, and having in transverse section an irregular triangular shape, the base of the triangle resting on the surface; nuclei are also present throughout the yolk, more especially near the periphery.

As was said in (3) the protoplasmic area next becomes more compact and flattened out against the side of the ovum, so as to form a kind of plate of fairly dense protoplasm which is closely packed with nuclei, and which lies on the surface at one side of the ovum through about the middle third of its length: this is shown in transverse section in fig. 13 (3), which is from one of the ova taken out in April.

A good many of the January eggs were of stages which came after this last. The protoplasmic area begins to grow round the surface of the egg until, as is shown in fig. 1, it covers nearly half the periphery. The nuclei in the central region of this protoplasmic area are two or three deep, but towards its edges the protoplasm thins gradually and the nuclei form only one layer. The ovum is closely packed with yolk, among which a few nuclei are irregularly scattered. The process of epibolic growth of the protoplasmic area continues, so that, as is shown in fig. 2, still more of the periphery of the egg becomes covered with the thin layer of protoplasm which may be called the blastoderm, until when the growth of the latter ceases only a very small portion is left uncovered.

The blastoderm now consists of a thin layer of protoplasm, in which a single layer of flat nuclei is present, extending round the whole periphery of the egg with the exception of a small space lying in the centre of one side of the egg in which the yolk is left uncovered. This uncovered space corresponds with the position of the future blastopore, and is, I believe, situated on the ventral side of the embryo, thus agreeing with other Arthropods, except the Scorpions, in which the blastopore is situated dorsally.

A change now takes place in the blastoderm behind and at the sides of the uncovered area. In the middle line behind this area a proliferation of the nuclei takes place extending some distance backwards, so that a keel-shaped mass of nuclei



embedded in a loose reticulum of protoplasm is present in about the posterior half of the ovum; this condition is shown in transverse section in fig. 3. The nuclei at the sides of the area also proliferate, as is shown in fig. 3 *a*, which represents a transverse section through this region from the same ovum as fig. 3, but is drawn under a higher power.

The proliferating mass of nuclei increases in size and occupies a larger portion of the surface of the ovum, and both nuclei and protoplasm are closer and more compact; a transverse section through the posterior half of such an ovum is shown in fig. 8. At the same time the protoplasm at the sides of the uncovered area become slightly inflected; this is shown in fig. 9, which is a transverse section through this region from the same ovum as fig. 8, but drawn under a higher power. The uncovered area thus forms a passage lined by the cells of the blastoderm, which have become inflected, and leading into the yolk; it may be spoken of as the blastopore, as is the case in *P. capensis* it is traversed by strands of protoplasm.

These two structures, i. e. the blastopore and the area of proliferating cells lying posterior to it, soon acquire very close resemblance to the blastopore and primitive streak of *P. capensis*, with which they are probably homologous. The blastopore increases in length and the protoplasm at its sides shows a true invaginate character, and a groove is present running from the posterior lip of the blastopore down the centre of the primitive streak. Three transverse sections through an egg of this stage are shown in figs. 5, 6, and 7. Fig. 5 passes through the blastopore at about the middle point of its length, where it is very clearly open; at this time it is about an eighth of the total length of the ovum. Fig. 6 passes through the region immediately behind the blastopore through the primitive streak and groove. Immediately beneath the primitive groove there is a small cavity bounded by the protoplasm of the primitive streak, the nuclei round it being arranged in a roughly columnar manner, and filled with very small yolk-spheres, among which are one or two nuclei; this



cavity is marked *c* in the figure. It ends blindly in front and behind, and probably is homologous with the area which Mr. Sedgwick (1) calls the polar area in *P. capensis*, which, both in position and structure, it closely resembles, with the exception of the fact of its being filled with yolk-spheres in the New Zealand species. Fig. 7 passes through the posterior end of the primitive streak, where it is thinning out, and the groove is much shallower. These three sections bear a very close resemblance to figs. 25 and 26 on Pl. V of Mr. Sedgwick's Monograph on the Cape species (1). The peripheral nuclei in the region of the blastopore and primitive streak have a more or less columnar form instead of lying flat against the side as they do over the rest of the ovum. The anterior part of the egg is enveloped in a single layer of flat nuclei.

In an ovum of a slightly later stage the blastopore has increased a little in length, the primitive streak is much larger and more marked, the nuclei being very closely packed, and the primitive groove is considerably deeper; the so-called polar area has disappeared. This stage is the latest which was present among the January eggs, except some quite old embryos which were almost ready for birth.

I have examined several series of sections of older embryos, i. e. in which they were developed, but have not thought it necessary to give an account of them, as the process of development seems to be similar to that of *P. capensis* described by Mr. Sedgwick (1).

The only point of interest in which it differs from that species is that the first somite (i. e. that of the præoral or antennal segment) opens by a duct to the exterior in precisely the same way and position as do those of the third to fifteenth segments, so proving it to be the nephridium of the segment with the same relations as those of the posterior ones. This is shown in figs. 10 and 11; in the former the opening of the duct to the exterior just outside the nerve-cord is shown, and in the latter, which is separated from the former by three sections, its opening into the somite. The probability of the nephridial nature of this somite was pointed out by Mr. Sedgwick.

Summary of the Results of my Investigations on the  
Development described in this paper and the  
previous one (3)

1. The ovum is heavily charged with food-yolk; the segmentation is on the centrolecithal type; the protoplasm is mainly at one pole of the egg, and in this protoplasm nuclei arise, probably by the division of the segmentation nucleus. The protoplasm forms a loose reticulum containing nuclei on the surface of the egg, which first extends over only a small area, but later spreads over the surface until, in the latest stage which I have, it covers about half the periphery of the egg.

2. In the latest segmenting ova there are small masses of protoplasm in the centre of the egg, which masses sometimes contain nuclei.

3. Shortly after the segmentation begins the yolk becomes divided up into a number of rounded segments, which, however, bear no relation to the true segmentation.

4. The central nuclei of those lying just beneath the periphery multiply much more rapidly than those over the rest of the ovum, thus coming to form a special area, which finally extends along about the middle third of the ovum, and consists of a loosely-reticulate mass of protoplasm containing a large number of nuclei, and having in transverse section an irregular triangular shape. Nuclei are present through the rest of the ovum, being more numerous near the periphery than the centre.

5. The triangular-shaped protoplasmic area becomes more compact and flattens itself out, forming a plate-like mass of protoplasm densely packed with nuclei on the surface of the middle third of the ovum. This plate is the blastoderm. The nuclei over the rest of the egg have undergone no change.

6. The blastoderm grows round the ovum till it covers about

one half of its surface, at which time it is thickest in the centre and thins gradually towards its edges.

7. The epibolic growth of the blastoderm continues until only a very small space in the middle of the ventral face of the ovum is left uncovered.

8. A proliferation of the nuclei behind the uncovered area in the middle line takes place, forming a (in transverse section) keel-shaped mass of nuclei extending along about the posterior half of the ovum. The nuclei at the sides of the space also proliferate.

9. The protoplasm round the space becomes inflected, and so forms a blastopore. The proliferating mass of nuclei or primitive streak increases in amount.

10. The blastopore increases in length considerably, and becomes more open. The primitive streak also becomes wider and deeper, and a groove—the primitive groove—appears along its centre. Beneath the primitive groove a small cavity filled with yolk and bounded by columnar nuclei, and apparently homologous with the polar area of *P. capensis*, appears.

11. The blastopore and primitive streak and groove increase and become more marked. The polar area disappears.

12. Up to this stage no trace of any cell-outlines is visible, but the protoplasm forms a syncytium, in which nuclei are irregularly scattered. At this point a large gap is present in my investigations.

13. A layer of yolk is present outside the embryo. This peripheral yolk becomes gradually absorbed, and various changes are undergone by the embryo (descriptions of which are given in (3), vide summary, p. 255) until it reaches the stage at which the absorption is complete, when the appendages begin to appear, &c.

14. The later development, i.e. after the appendages are formed, is similar to that of *P. capensis*, the only interesting point of difference being that the duct of the first somite opens to the exterior.



### General Considerations.

The investigations which I have made on the January eggs of *Peripatus novæ-zealandiæ*, although the stages examined were few, nevertheless throw a good deal of light on the subject of the early history of the development. In my former paper (3) I remarked upon the strange dissimilarity which existed from the segmentation stages up to quite late ones between the three species of *Peripatus* whose developmental history has been at all fully worked at. In the cases of *P. capensis* and *P. novæ-zealandiæ* at all events this remark now requires modification. The developmental history of the latter is now fairly complete as far as the gastrula stage, and up to that point its resemblance to that of *P. capensis* is very marked. As I pointed out before (3) the segmentation is very similar, the main differences being easily accounted for by the presence of the yolk in the one species, and its almost total absence in the other. I have now shown that in the New Zealand species the ectoderm, which at first covers only a portion of the ovum, gradually grows round until only a small space on its ventral side remains uncovered, and at this spot an invagination takes place forming the blastopore, behind which in the middle line the primitive streak and groove are present. In all these stages the resemblance to the corresponding ones of *P. capensis* is very striking, the main difference consisting, as in the segmentation stages, in the presence of the yolk. This similarity is clearly seen on a comparison of Mr. Sedgwick's figures on Pls. IV and V (1) and my own (3). In fact it seems somewhat strange that the almost total loss of the yolk, which must almost certainly have been possessed originally by the Cape species, should have apparently been accompanied by so few modifications in its development, since so important a change of conditions might have been expected to exert a considerable influence on the latter.

Unfortunately there are many stages wanting between the gastrula stage and the next one which I have described in my



previous paper (3). In it one of the most remarkable features was the presence of the yolk outside the embryo, between it and the vitelline membrane. It might be more correct and intelligible to consider this as ectodermic yolk. In *P. capensis* protoplasmic strands are present, passing from the ectoderm to the egg-shell, especially in the region of the dorsal hump, and these very probably indicate that ectodermal yolk was present at one time in this position. In the last chapter (*supra*, p. 125) of his Monograph of the Cape species, Mr. Sedgwick states that the ectoderm is much vacuolated and contains globules which he believes to be yolk up to a comparatively late stage of development. Thus it seems probable that both species were possessed of ectodermal yolk. In the gastrula stage in both species there is no sign of any trace of yolk which probably therefore arises later. In *P. novæ-zealandiæ* this yolk is so thick that it completely obscures the external characters, which cannot be made out in surface view till the stage at which the appendages are forming when the ectodermal yolk is almost completely absorbed. As to the mode and time of origin of this ectodermal yolk in *P. novæ-zealandiæ* I am not able to make any statement, as in the youngest egg in which it is present it is already well formed, and constitutes a very thick layer; and I do not know whether it is derived in some way from the central yolk, or whether it arises as a fresh formation in the ectoderm cells. However, the fact that in both species it is absent in the gastrula stage and appears later seems to point to its being an ancestral feature in the development. This, as well as many other points of interest in the development of this interesting species, will unfortunately have to remain unexplained until someone shall be fortunate enough to obtain embryos of the intermediate stages.

Summary of Dates of Embryos which are figured in this paper and the previous one (4).

Previous paper (4):

Figs. 1—10.—December. Figs. 11—20.—April. Figs. 21 *a, b, c.*—July. Fig. 22.—July. Fig. 23.—December. Fig. 24.—December. Fig. 25.—July. Fig. 26.—July.

This paper:

Figs. 1—9.—January. Fig. 10.—July. Fig. 11.—July.

Thus, speaking generally, the ages of the embryos received in the various months are:

December.—Stages from unsegmented ova up to that at which nuclei were present at intervals just beneath the surface round about half the ovum.

January.—From late segmentation up to gastrula stage.

April.—Two embryos showing the beginning of the formation of the blastoderm, and also several stages with ectodermal yolk.

July.—Stages in which the appendages are being formed up to embryos which were ready for birth. There were also newly-born young.

Conclusion arrived at as to Time of Development.

Probably the ova pass from the ovary into the uterus in December, and the young are born in July, the development thus occupying a period of about eight months.

This, though apparently usually the case, cannot be universal since in each lot there were one or two females which contained embryos ready for birth, and also the embryos in one female vary somewhat in age.

This statement as to the period of gestation has already been made by Mr. Sedgwick (2).

LIST OF PAPERS REFERRED TO.

- (1) SEDGWICK, A.—“A Monograph of the Development of *Peripatus capensis*.” These Studies, vol. iv.
- (2) SEDGWICK, A.—“A Monograph of the Species and Distribution of the genus *Peripatus*.” These Studies, vol. iv.
- (3) SHELDON, L.—“On the Development of *Peripatus novæ-zealandiæ*.” These Studies, vol. iv, pp. 230-262.

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EXPLANATION OF PLATES XXVII & XXVIII,

Illustrating Lilian Sheldon's paper, “On the Development of *Peripatus novæ-zealandiæ*.”

*List of Reference Letters.*

*Bl.* Blastoderm. *Btp.* Blastopore. *c.* Cavity, corresponding to polar area of *P. capensis*. *Pm. A.* Protoplasmic area. *Pr. Gr.* Primitive groove. *Pr. St.* Primitive streak.

All the figures were drawn with Zeiss's camera lucida; Figs. 3 *a* and 9 were drawn under Zeiss's oc. 2, obj. cc; Fig. 4 under Zeiss's oc. 2, obj.  $\Delta$ ; and the rest under Zeiss's oc. 2, obj. B.

FIG. 1.—Transverse section through an ovum, in which the blastoderm has grown nearly half way round the yolk.

FIG. 2.—Transverse section through the centre of an ovum, in which the yolk is nearly covered by the blastoderm.

FIG. 3.—Transverse section through an ovum, in which the primitive streak is beginning to arise.

FIG. 3 *a*.—Transverse section through the portion of the same ovum which is not covered by the blastoderm, drawn under a higher power.

FIG. 4.—Transverse section through the centre of a young ovum before the formation of the blastoderm, showing the multiplication of the nuclei in one region near the periphery.

FIGS. 5, 6, and 7.—Three transverse sections through an ovum in which the blastopore is well formed.

Fig. 5. Through the blastopore.

Fig. 6. Just behind the blastopore.

Fig. 7. Near the posterior end of the primitive streak.

FIG. 8.—Transverse section through an ovum with a primitive streak.

FIG. 9.—Transverse section through a portion of the same ovum, to show the invagination at the blastopore beginning at the anterior end of the primitive streak. Drawn under a higher power than Fig. 8.

FIG. 10.—Transverse section through an embryo with appendages, to show the duct of the first somite opening to the exterior.

FIG. 11.—Transverse section through the same embryo four sections posterior to Fig. 10, to show the duct opening into the first somite.

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Fig. 1.



Fig. 2.

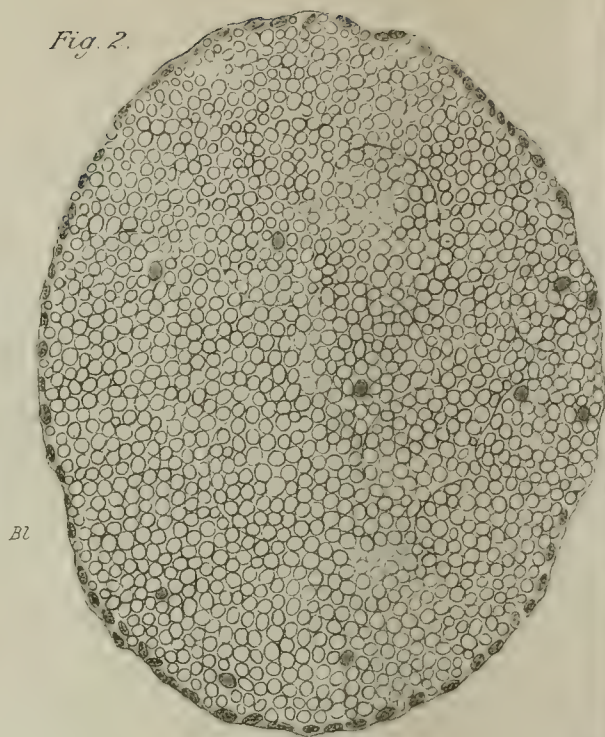
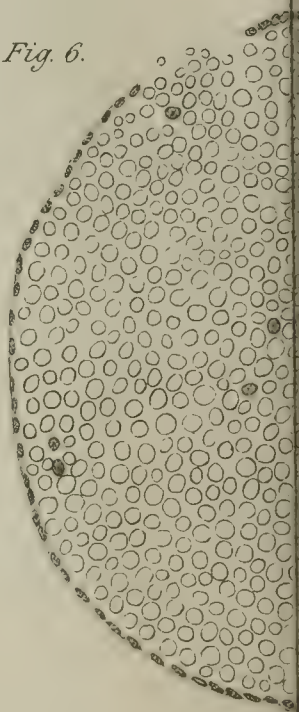


Fig.

Fig. 5.



Fig. 6.



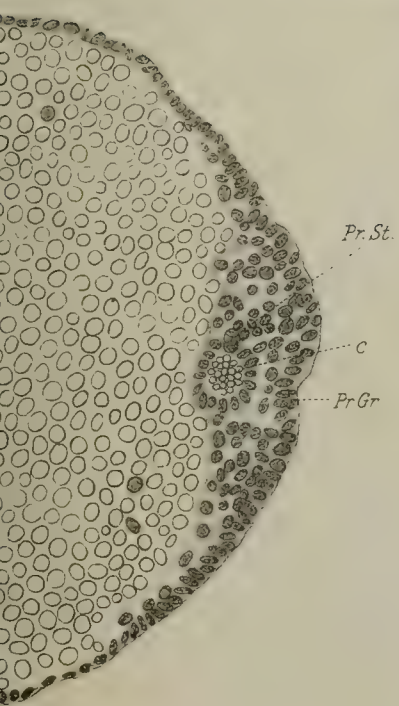
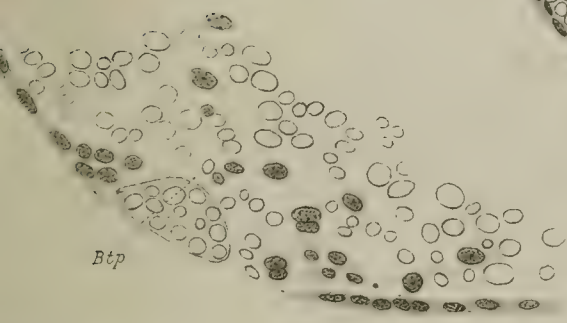
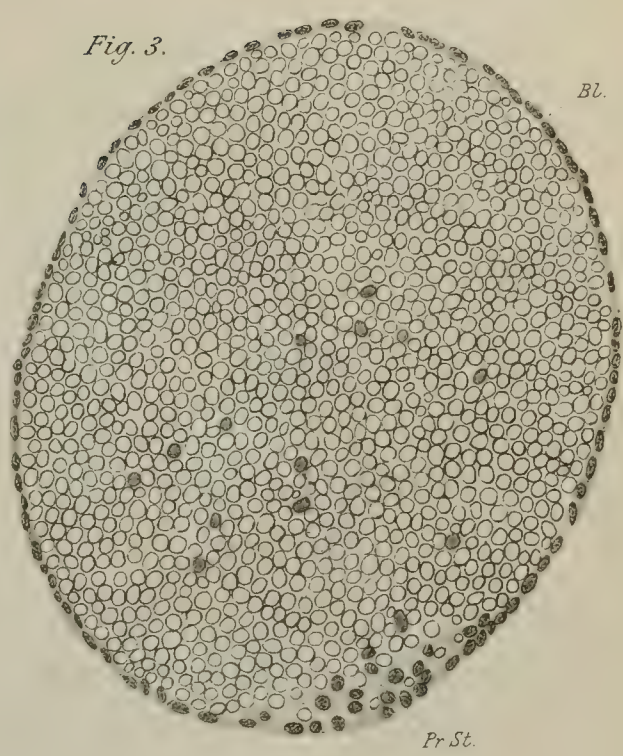
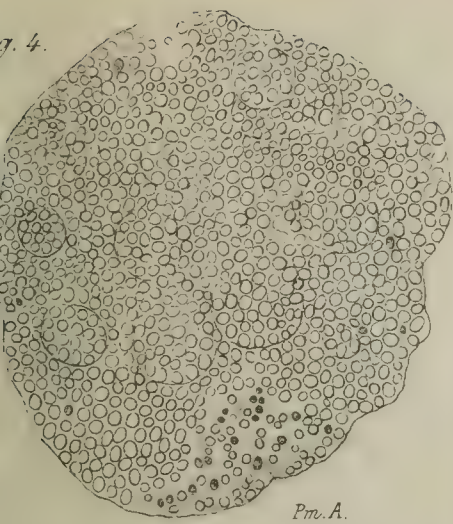


Fig. 7.

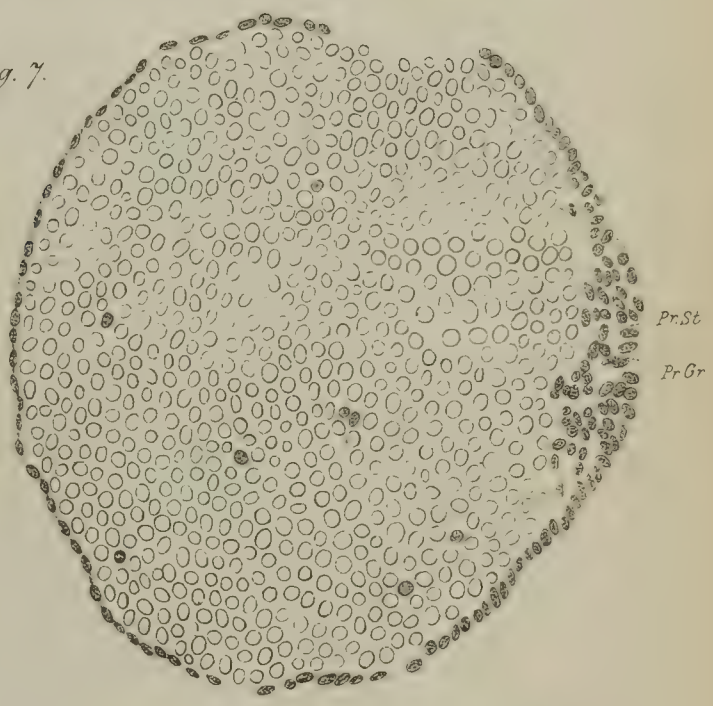






Fig. 8.

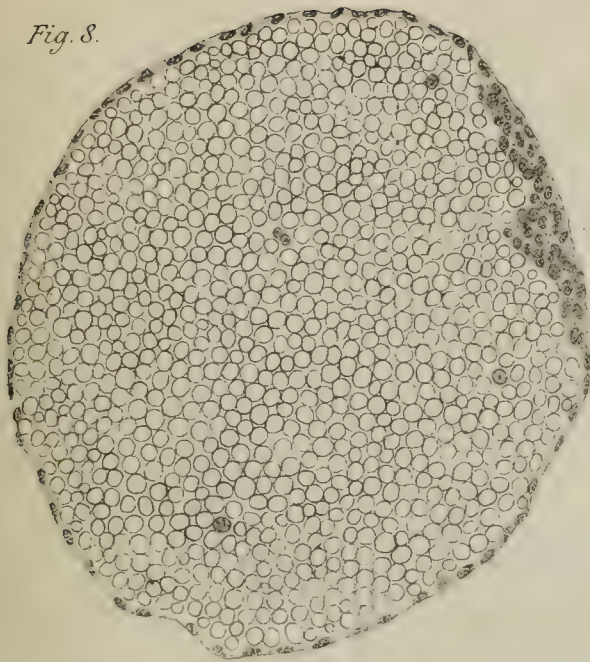


Fig. 9.

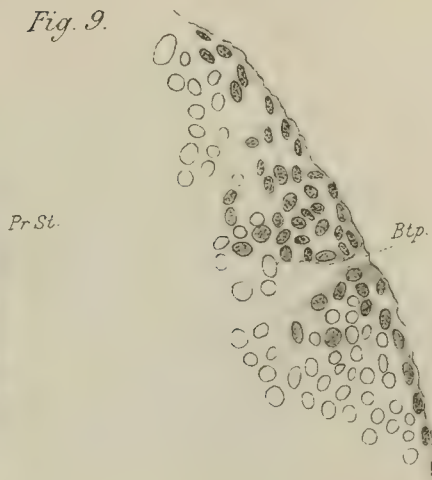


Fig. 10.



Fig. 11.





## The Maturation of the Ovum in the Cape and New Zealand Species of Peripatus.

By

**Lilian Sheldon,**

Bathurst Student, Newnham College, Cambridge.

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With Plates XXIX, XXX and XXXI.

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### DESCRIPTION OF MATERIAL.

THE species of which I had the most complete supply is *Peripatus capensis*, and consequently I have been able to obtain a more satisfactory account of the events attending the maturation of the ovum in it than in either of the other two.

The material consisted of ovaries taken from females in July, September, October, December, January, and March. During April females were killed almost every day, and both the ovary and the eggs in the uterus were preserved, so that I have a large number of ova before the beginning of the segmentation. The supply of *P. Balfouri* is smaller, but of that species also there was a fair number of præ-segmentation ova preserved during April.

Of *P. novæ-zealandiæ* I have a much smaller supply. It consists of a few ovaries of July, April, December, and January, and some unsegmented ova taken from the uterus in December.

The specimens were preserved in various ways, and the results obtained in all the methods were the same. My work was done entirely on sections, of which it was easy to obtain

complete series, as the preservation was in almost all cases satisfactory.

All my material was provided for me ready preserved by Mr. Sedgwick, who also placed at my disposal a number of series of sections which he had cut of the early stages of the Cape species. For this kindness, as well as for much valuable advice and assistance which he gave me throughout my work, I wish to express my very sincere thanks.

#### PERIPATUS CAPENSIS.

Structure of the Ovary.—The ovary has the same general anatomical structure in all the species of *Peripatus* in which it has been hitherto described.

In *P. capensis* it consists of a pair of tubes lying parallel to one another and to the long axis of the body, and uniting anteriorly, where the ovary is attached to the ventral wall of the pericardium. Posteriorly they also unite into a short common duct, which almost immediately divides into the two oviducts.

The epithelial lining of the ovary is of two kinds (v. fig. 1). On the inner side of each tube it is thin and flat, with very distinct nuclei; while on the outer it is very thick (figs. 1 and 3). It is this thick mass which is the germinal epithelium.

Towards the end of April, i. e. shortly after all the ova have passed from the ovary into the uterus, the germinal epithelium forms a very thick mass, consisting of protoplasm with nuclei, and the remains of spermatozoa scattered through it (fig. 1). The protoplasm shows no cell outlines even when examined under a high power of the microscope, and is then seen to consist of a loose, irregular, spongy mass. A small portion of the ovarian wall at the junction of the germinal with the thin epithelium is shown in fig. 2, which was drawn with Reichert's  $\frac{1}{15}$  oil immersion lens; on the side which lies towards the body cavity there is an irregular layer of nuclei lying more or less parallel to the surface, and on that which is directed towards



the cavity of the ovary the nuclei are pear-shaped, and have a roughly columnar arrangement, while the protoplasm itself has a very irregular outline fraying out into the cavity of the ovary, is very reticulate and spongy, and is traversed by wavy striæ, which are probably elastic fibres. The protoplasm of the whole of the germinal epithelium possesses a similar structure. The nuclei at this time are all alike, there being no distinction between those which will become ova and the remaining ones, so that it seems probable that any nucleus may subsequently become an ovum, and that there is no differentiation into germinal and follicle cells, &c. At this time the only spermatozoa which are present in the female generative apparatus are a few scattered ones in the cavity of the ovary, and a few, which are generally arranged in groups, lying in the protoplasmic meshwork of the germinal epithelium.

I have not examined any ovaries of May or June, but from July onward up till the time the ova are about to pass into the oviduct the ovarian tubes are crowded with a thick matted mass of spermatozoa (figs. 3 and 4). Like Mr. Sedgwick (14), I have never found any spermatozoa in any other part of the female generative organs.

The structure of the ovary of *P. capensis* differs from that of *P. Edwardsii*, as described by Gaffron (9), since in the latter the whole ovarian tube is lined by germinal epithelium, the ovary being embedded in the stroma, and hence the ova lie all round the cavity instead of along the outer side only.

**The Ovarian Ovum.**—In July the ova are perfectly distinguishable from the other cells of the germinal epithelium. Each ovum (v. fig. 3) possesses a central nucleus surrounded by a layer of dense granular protoplasm, and lies on the outer side of the ovarian wall, where it forms a short, blunt projection into the body-cavity. The nucleus is large, has a central position, and is distinguished from the cell substance by staining rather more deeply; it is granular and contains a not very clearly-defined nucleolus. There is no distinct line of demarcation between the protoplasm of the ovum and that of

the rest of the germinal epithelium, the limit being marked only by the density of the former.

By September (v. fig. 4) the ovum has increased considerably in size, has acquired a definite oval shape, and is enclosed in a very thin shell. The nucleus is round, has a central position, and encloses a round excentric nucleolus. The peduncle connecting the ovum with the ovarian wall has become larger and is still many cells thick.

An ovum of this date (September), with its stalk, is shown in fig. 5: the nucleus contains a protoplasmic reticulum with special aggregation of chromatin at the junctions of the strands, and also a round, excentric nucleolus.

From this time onwards the ova gradually increase in size, and the peduncles grow longer and thinner. The nucleus and nucleolus also become larger and the shell acquires considerable thickness.

In the youngest ovum (v. fig. 8) which I have found in the ovary of April, the nucleus still has a central position and contains a large round nucleus, which is slightly excentric, stains very deeply, and encloses some highly refractive chromatin and some very small vacuoles. The nucleus is granular, and not very definitely marked off from the cell-protoplasm; but I am not able to trace any distinct connection between the reticula of the two. The shell is very thick. The cell-protoplasm has a granular structure, and contains numerous very minute, highly refractive globules, which appears to be yolk. The stalk is long, and is, through most of its length, two cells thick.

The next event is the travelling of the nucleus from the centre to the periphery of the ovum, at the side removed from the point of attachment of the stalk. The protoplasm also loses its dense character and becomes looser. The nucleus has a definite wall, which is continuous with the meshwork of the protoplasm.

In the next stage (v. fig. 9) the protoplasm is still less dense and more loosely reticulate; the nucleus lies quite peripherally, is homogeneous in structure, and has lost its nucleolus.

In addition to the minute yolk-spherules scattered through the protoplasm, there are a few larger bodies lying just below the shell, which stain deeply, have a homogeneous structure, and are probably of a yolky nature. The cells of the lower end of the stalk have begun to grow round the outside of the egg so as to form a follicle, which at this stage extends round about one third of its circumference.

The nucleus, as is shown in fig. 6, next becomes irregular in outline, and is thrown into folds, which project into the surrounding protoplasm. These projections, with depressions between them, occur all round the nucleus. This change in the nucleus is probably the forerunner of its total disappearance, which in the next stage will be described as having disappeared, though I have not been able to observe the further steps in the process in this species. In *P. Balfouri*, however, I have a further stage in its disappearance, in which the nuclear wall is completely lost, the position of the nucleus being indicated by a dense mass of protoplasm, which at its edges is continuous with the loose protoplasmic reticulum of the egg, and which contains in its centre some irregular chromatic particles: this condition is shown in fig. 7. By a still further diffusion and breaking up of this dense mass of protoplasm, it is easy to conceive how the nucleus and even its former situation might become invisible.

In the next stage the nucleus is invisible, and the follicle completely surrounds the egg, consisting of a layer of flat cells which closely adhere to the eggshell; just within the eggshell a few irregular, rather deeply-staining aggregations are present in the protoplasm of the ovum. These may be the remains of the nucleus which have become scattered through the egg, since no such aggregations are present in the former stage in which the nucleus itself was visible.

The next stage is shown in fig. 8. It differs from the last only in the fact that the follicle does not adhere to the eggshell, but is separated from it all round, so that the ovum lies loose in a hollow vesicle, which is attached to the ovary by a long thin stalk. At this stage the cellular nature of the follicle



is hardly discernible, owing to its great thinness; a few very flat nuclei can, however, be distinguished in it. The ovum at this stage is completely surrounded by its thick shell, and I was not able to observe any micropyle or break in the latter for the entrance of the spermatozoon. Apart from the fact that the egg is oval in shape, and consequently possesses a long and a short axis, there was no means of distinguishing any difference in the surfaces, or any pole of impregnation.

This is the oldest ovum which I have found in the ovary. I suppose that it now passes into the cavity of the ovary through the stalk, which must acquire a cavity for the purpose. The only indication of such a process which I have observed is that in some cases the stalk has a vacuolate structure, and is irregularly two cells thick. In fact, I have never found an ovum either in process of passing into or in the ovary, but the next stages of ova are in the uterus. From this I infer that the process must be one of extreme rapidity, as I have ovaries which were preserved at various times through April.

Since, as has been already stated, spermatozoa are present in great abundance in the ovary and in no other part of the female organs, it may be assumed that fertilization of the ovum takes place in its passage through the ovary, and hence I have never observed the process, although, as I shall describe shortly, I have several ova in which the male pronucleus is clearly seen.

**The Uterine Ova.**—There is a very remarkable difference in size between the oldest ovarian ovum and the youngest uterine one. The greatest length registered for the former is .26 mm., while the smallest ovum found in the uterus measured .6 mm., or more than double. An analogous but even greater proportional difference is stated by Mr. Caldwell (6) to occur in *Monotremata*, where he alleges it to be due to the absorption of fluid from the uterine wall, and probably it is produced by the same cause in the case of *Peripatus*.

I have two uterine eggs in which the nucleus was absent. In one of them the shell adhered closely to the protoplasm of the egg, and was not separated from it by a space as is the



case in older eggs; the protoplasm formed a very clear reticulum, the strands of which stained well and anastomosed with one another to form a very definite network, on and occasionally between the strands of which small, round, highly refractive, deeply-staining bodies are present. The spaces between the strands are sometimes occupied by a granular faintly-staining substance, which is probably a coagulum. In this ovum there was no trace of any structure in the least comparable to a nucleus.

In the other non-nucleated ovum the strands of the protoplasmic reticulum are very clear, but the highly refractive particles are not present, but there are some angular homogeneous bodies present in the protoplasm. A transverse section of this ovum is shown in fig. 10. As is there figured at one point on the surface a slight prominence is present, and in it there are a few fine threads of chromatin lying at right angles to the surface of the ovum. This may be caused by the entering in of a spermatozoon, but I am not able to state this definitely. A similar structure was present in one or two other ova, but in no case was it so clear as to enable me to state definitely that the process was one of fertilization. At first sight it might appear to be due to the formation of a polar body, but I do not think it is so, as in all the cases which I have of that process, which I shall describe below, the appearances are quite different to the above.

The next stage is that at which the germinal vesicle is again present; as to its formation and origin I have no observations. A transverse section through an egg of such a stage is shown in fig. 12. In it the protoplasmic reticulum is very clearly shown with small chromatin granules lying on the strands. On the periphery at one side in the middle of the long axis of the ovum there is a small mass of dense protoplasm, which at its edges passes into the loose reticulum of the ovum. In its centre it is somewhat denser, and a few chromatin granules are there cut through, while in a few sections respectively before and behind the chromatin the protoplasm shows indications of a radiate arrangement which is due to the stars at the ends of

a spindle, the chromatin representing the nuclear plate. The spindle in this case is cut transversely to its long axis, the section figured passing through the chromatin of the nuclear plate. Fig. 11 represents a section through an ovum of similar stage, in which the spindle is cut vertically; in this case the spindle lies with its long axis at right angles to the surface of the ovum beneath which it lies. The same spindle is shown more highly magnified in fig. 15.

The spindle next changes its position so as to lie parallel to the surface of the ovum; this is shown in fig. 16.

The chromatin of the nuclear plate separates into two layers, a condition which is shown in fig. 17; and the two plates of chromatin leave the centre of the spindle and gradually approach its two ends respectively. A spindle at this stage is shown in fig. 18.

A protuberance now appears on the surface near one end of the spindle, into which the latter passes, and by a gradual constriction this protuberance becomes separated off and forms the first polar body, the chromatin of the spindle still remaining clearly visible in it. Owing to the long axis of the spindle being parallel to the surface of the ovum, the polar body does not lie directly above but to one side of it (v. figs. 16 and 19).

The nucleus now returns to a resting stage (v. figs. 19 and 20 *a*), when it has an oval form, stains slightly deeper than the surrounding protoplasm, and contains several chromatin bodies. It does not at this stage possess a clear or deeply staining wall. The nucleus at this stage is shown in fig. 19, where also the position of the first polar body, to one side of and not directly above it, is also shown.

The nucleus now again assumes the spindle form, and the second polar body is formed in a manner exactly similar to the first.

In fig. 11 the male pronucleus is seen to be present lying at the opposite side of the ovum from the germinal nucleus. It is very small and oval, and contains a small amount of chromatin. It lies quite at the periphery of the ovum, close within the eggshell. The protoplasm round it is marked with striæ

which radiate from the pronucleus towards the centre of the egg.

In all the other ova of *P. capensis* in which the formation of polar bodies was taking place, I was unable to see any pronucleus, although I believe that that structure must be present in them, since it seems certain that fertilization must take place in the ovary. In several cases there were special aggregations of protoplasm, in one of which the male pronucleus may have been present, although I was not able to distinguish it, and I am inclined to think that for a short time after entering the ovum it is invisible, possibly from a lack of chromatin.

In the next stage, when the polar bodies are both formed, the male and female pronuclei are both present as very well-marked structures. Two sections through an egg of this stage are shown in figs. 14 *a* and 14 *b*. Fig. 14 *a* passes through the second polar body and the female pronucleus; the former lies in a depression on the surface of the ovum and is not completely separated from it, being connected with its protoplasmic reticulum; it contains three chromatin granules. Just below it lies the female pronucleus, which is now in the resting condition, and has begun to assume the lobed structure, which was described by Mr. Sedgwick (14) as being so characteristic of the segmentation nuclei, and is divided by a septum into two compartments, in each of which are a few chromatin granules. It is not surrounded by any special dense protoplasm, but its wall is continuous with the general loose reticulum of the egg. Fig. 14 *b*, which is several sections removed from fig. 14 *a*, passes through the male pronucleus, which is now a very prominent feature in the egg. It is round in shape, and lies near the centre of the egg, being connected with the periphery at the side removed from the female pronucleus by a denser mass of protoplasm, which in transverse section is roughly wedge-shaped. In these two figures only the protoplasm in the neighbourhood of the pronuclei is figured. Seen under a high power, the male pronucleus is seen not to be sharply marked off from the extra-nuclear substance,



strands connecting the two being clearly visible. I have found the male pronucleus in this condition in three ova of *P. capensis*.

I have seen no ova of *P. capensis* in which the union of the pronuclei is taking place, though I shall shortly describe one of *P. Balfouri*, in which the male and female pronuclei lie close together in the centre of the ovum, and are apparently about to conjugate. In the next stage of *P. capensis* the union has apparently taken place, and the nucleus is a large lobed structure lying some little way from the periphery. It is not surrounded by a large and definite mass of denser protoplasm, but only by a very narrow layer, which almost immediately passes off into the loose reticulum which fills up the rest of the ovum.

In the next stage the segmentation nucleus is fully formed; it lies near the periphery, and is surrounded by a specially dense mass of protoplasm, which, as Mr. Sedgwick (14) has stated, causes the dark patch which is seen on these ova, by means of which, even after preservation, the præ-segmentation ova can be readily distinguished from those in which the segmentation nucleus is present. I have not figured ova of this stage, as Mr. Sedgwick (14) has already done so (Pl. III, figs. 8 and 11).

#### PERIPATUS BALFOURI.

The phenomena connected with the maturation and fertilization of the ovum in *P. Balfouri* are very much the same as in *P. capensis*, and therefore I shall merely describe the differences between the two, and one or two stages which I have found in the former, which were wanting in the latter.

Structure of the Ovary.—A section through one half of the ovary is shown in fig. 22; its structure in the main is the same as that of *P. capensis*, but the germinal area is much narrower, being confined to a narrow strip along the outer side of each ovarian tube. The non-germinal epithelium is also very much thinner; and, in fact, has the appearance of a membrane with small bulgings on it caused by the nuclei.



**Ovarian Ova.**—Three ova of December are shown in fig. 22, and are very similar to the September ones of *P. capensis*; in fact, up till nearly the beginning of April, the ova of the two species are indistinguishable.

Fig. 23 is from a section of an ovum in which the germinal vesicle has acquired the full size which it attains while still in the centre of the ovum. The germinal vesicle has a somewhat different structure from that of *P. capensis* of the same stage (cf. fig. 8); it has a groundwork which has no structure, and does not stain, but is fairly definitely marked off from the rest of the egg, while in it lies a deeply-staining, irregular network, which has a rather coarsely granular appearance, and a round excentric large nucleolus, or germinal spot. Small round, highly refractive yolk particles were present in the egg protoplasm.

The next ovum which I have figured is shown in fig. 24; unfortunately it had become broken off from the ovary before it was cut, so that I could not see its relation to its stalk or follicle. It was round in shape; it had a thick shell, which was broken in one place, probably at the point of attachment to the ovary. There was no trace of a germinal vesicle or germinal spot. The protoplasm formed a loose reticulum with a granular structure, and through it were scattered round homogeneous bodies, which I believe to be yolk, but I have no observations on their origin.

**Uterine Ova.**—In the youngest ova in the uterus there is no sign of germinal vesicle or male pronucleus. The protoplasm forms a loose reticulum and contains yolk-spheres.

The reappearance of the germinal vesicle and the formation from it of two polar bodies takes place as in *P. capensis*. In two ova in which the formation of polar bodies was taking place, the male pronucleus was present as a small chromatin body lying at the periphery of the ovum opposite the side where the germinal vesicle was situated, and surrounded by a small zone of clearer, less deeply staining protoplasm than that of the main part of the ovum; this condition of the male pronucleus is shown in fig. 21. There was no radiate arrange-

ment of the surrounding protoplasm such as was observed in the very young male pronucleus of *P. capensis*. The next appearance of the male pronucleus is similar to that shown for *Peripatus capensis* in fig. 14 *b*, where it lies near the centre of the egg and is large and nearly spherical. A section through such an ovum of *P. Balfouri* is figured by Mr. Sedgwick (14) (Pl. III, fig. 1), and consequently I have not thought it necessary to draw it again.

Fig. 25 is from a section through an ovum in which the male and female pronuclei lie near the centre of the ovum, and are apparently about to unite. The female pronucleus does not stain, with the exception of its wall, and some chromatin particles which are present in it; it consists of several lobes separated from one another by prolongations of the wall inwards. The male pronucleus stains very deeply, and, like the female, has a lobed structure and contains some chromatin granules. The protoplasm round the pronuclei is rather denser than over the rest of the ovum. Yolk-spheres are scattered in the protoplasm.

The actual union of the pronuclei I have not seen. The resulting segmentation nucleus is similar in all respects to that of *P. capensis*.

#### PERIPATUS NOVÆ-ZEALANDIÆ.

The differences between the stages passed through in the maturation of the ovum of the Cape and New Zealand species are considerable, owing mainly to the large amount of food-yolk in the latter.

Structure of the Ovary.—The ovary resembles that of *P. capensis* in structure. It is attached, however, along its whole length to the ventral wall of the pericardium, instead of by its front end only as is the case in the Cape species. In one ovary from an animal which was opened in December, there was a good deal of yolk, which lay mostly just below the non-germinal part of the epithelium. A transverse section through this ovary is shown in fig. 26; the only connection

between the two sides of the ovary throughout their middle region is by means of the wall of the pericardium to which they are both attached. The yolk is coloured yellow. There are never any spermatozoa in the ovary, these being in the receptaculum seminis, which is present in this species. In all but a very few cases I have found the receptaculum tightly packed with spermatozoa.

**Ovarian Ova.**—As in the other species the ova arise from the nuclei of the germinal epithelium.

The youngest egg which I have observed was situated on the outer side of the germinal epithelium bordering on the body-cavity. The protoplasm, which was granular, formed a narrow band surrounding a nucleus which stained more deeply, and was coarsely granular. A nucleolus was present, placed almost centrally.

The egg grows in size, both nucleus and cell-substance taking part in the process. The nucleus acquires a vacuolate structure, the substance between the vacuoles staining deeply and having a homogeneous appearance; the nucleolus also has grown slightly. The egg projects from the ovary, being situated at the end of a short stalk which is formed from some of the cells of the germinal epithelium.

The egg continues to grow, and a further change takes place in the character of the nucleus, which consists in the aggregation of the deeply staining vacuolated tissue towards its periphery, thus leaving a small central area round the nucleolus.

This aggregation progresses still farther and the tissue loses its reticular character and forms for the nucleus a solid widish wall, which is homogeneous and stains deeply. The centre of the nucleus does not stain, with the exception of an irregular faintly staining reticulum, and the nucleolus which is placed about in its centre. The nucleolus is round, stains very deeply, and contains some small vacuoles and a number of small round bodies which stain even more deeply and are very highly refractive. The egg-protoplasm at this stage is granular, and contains numerous verysmall yolk-globules, which resemble those which are present in the Cape species at a similar stage,



and seem to arise in the protoplasm itself. A transverse section of an ovum at this stage is shown in fig. 27. As will be there seen, the egg is now surrounded by a thin shell.

The nucleus now loses its evenly spherical form and becomes crinkled in outline. This appears to be due to the passage out from it of portions of its substance which pass into the extra-nuclear tissue in the form of round bodies of various sizes. These bodies, like the portion of the nucleus from which they are formed, are perfectly homogeneous, and stain with picrocarmine a deep yellowish red. This process is shown in fig. 28. The small yolk-globules are still present (coloured yellow). The shell has increased in thickness.

This process continues until all the wall of the nucleus is dispersed, the central clear part appears to blend with the egg-protoplasm, and the nucleolus remains behind lying in the protoplasm. This condition is shown in fig. 29. The round spheres derived from the nucleus remain unchanged. I believe that these round spheres form part of the yolk of the ovum, which question I shall further discuss later on in this paper.

All the above stages were very common and occurred to a greater or less extent in all the ovaries which I cut of April, July, and December, but the older stages, which I shall now describe, were only found in the ovary in December, and not in either April or July, a fact which supports the statement which I made in a previous paper (16, p. 272) that the ova probably pass into the oviduct in December.

Fig. 31 represents a transverse section through an ovum in which a small amount of yolk is present; this is coloured yellow in the diagram. A very obvious thing in this ovum is the entire absence of any definite boundary line between the follicle and the ovum itself, in fact, they pass into one another imperceptibly. There is a small amount of yolk present in the form of scattered spheres throughout the protoplasm of the ovum, which latter has a reticular and vacuolate character. There are also in the protoplasm small round or oval nuclei which in every respect resemble those of the follicle, and it seems almost



certain that these must have migrated from the latter, a process which would be simple in the absence of any separation between the ovum and the follicle. A few yolk-spheres were present in the tissue of the follicle itself. There was no trace of any germinal vesicle or germinal spot. The shell was thin. This ovum measured 3 mm. in its greatest diameter; as I neglected to measure these eggs before cutting, I am not able to state their length.

At the next stage on which I have observations, and which was found in an ovum from the same ovary as the last, there is a considerable increase in size, the ovum measuring .5 mm. in diameter. This increase seems to be due principally to a much greater abundance of yolk-spheres in it, the protoplasm being distributed among them as a very loose or sparse reticulum. The most remarkable fact about the ova of this stage is that the stalks by which they are connected with the ovary are hollow. One of these eggs is shown, in section, in fig. 32. As is there shown, the wall of the follicular stalk thins out where it reaches the ovum, and passes imperceptibly into its wall. In the hollow of the stalk there are a large number of yolk-spheres and a few nuclei, resembling those of the walls of the stalk, which appear to be passing down it into the ovum from the ovary, which contains in its cavity a large amount of yolk, as is shown in fig. 26, which represents a transverse section through this ovary. There are a few nuclei of the walls of the stalk, which appear to be about to be detached and pass into its cavity. There are none of these small nuclei in the deeper part of the ovum, from which I infer that they, together with those which had migrated from the follicle in the previous stage, became converted into yolk.

In the next stage, a transverse section through an ovum of which is represented in fig. 30, there has been a slight increase in size, the diameter being .56 mm. This ovum is completely filled with yolk, and no protoplasm is present, except in the form of a large, nearly round nucleus, which lies just beneath the point of attachment. This nucleus stains deeply and uniformly, with the exception of a few more deeply staining

threads and chromatin granules. The ovum is completely surrounded by a thin shell, which separates the ovum from its stalk. The egg-protoplasm is completely obliterated by the closely packed yolk-spheres, and there is no trace in it of nuclei from the follicle or stalk, these having probably become converted into yolk.

This is the oldest ovum which I have found attached to the ovary. The youngest ovum which I found in the uterus contained no nucleus, was surrounded by a thick shell, and was closely packed with yolk.

The subsequent stages, from that in which the first segmentation nucleus is present, have been described in a previous paper (16).

I have never observed the formation of polar bodies in this species, nor have I ever observed them on the surface of the ovum in later stages, as might be expected, if they were present.

I have never observed the process of fertilization, nor do I know where it takes place; but from the fact that I have never found spermatozoa in the ovary, while they are very plentiful in the receptacula seminis, I would suggest that the egg is fertilized in the oviducts in the region of the receptacula.

I have never found an ovum either in the ovary or upper part of the oviducts, and it is very probable that, from the large amount of food-yolk in the egg, a spermatozoon after entering it would easily be obscured from notice.

#### Summary of Events in the Maturation and Fertilization of the Ovum of *P. Capensis* and *P. Balfouri*.

1. The ovary consists of a pair of tubes lying parallel to one another and uniting anteriorly. Posteriorly they also unite into a short common duct, which almost at once divides into the two oviducts. The ovarian tubes are lined along the inner side by a flat epithelium, which is thinner in *P. Balfouri*

han in *P. capensis*, and on the outer by the thick germinal epithelium, which is narrower in *P. Balfouri* than in *P. capensis*.

2. The ova arise by a growth of some of the nuclei of the germinal epithelium; apparently any of its nuclei may give rise to ova.

3. The ova by July lie at the surface of the ovary, with which they are connected by short thick stalks. Each ovum has a large, round, central nucleus with an excentric nucleolus, surrounded by a layer of protoplasm which is not separated from the protoplasm of the germinal epithelium.

4. By September the stalks have increased in length, so that the eggs project farther into the body-cavity. The ova have increased in size and are surrounded by a thin shell on all sides.

5. The ova continue to increase in size, and small round, highly refractive granules of yolk appear in the protoplasm. The nucleus or germinal vesicle of *P. capensis* has a uniform granular structure, that of *P. Balfouri* does not stain with the exception of a deeply-staining irregular network in it. An excentric nucleolus or germinal spot is present.

6. The nucleus passes to the periphery, and is large and round, and almost homogeneous, with only slight traces of a reticulum.

7. The germinal spot disappears.

8. The wall of the germinal vesicle becomes irregular in outline and then disappears, its contents becoming fused with, and indistinguishable from, the cell-substance. In *P. Balfouri* yolk-spheres have made their appearance.

9. The ovum becomes detached from the follicle, which has grown all round it, so lying in a hollow vesicle.

10. It probably passes down the stalk into the ovary and there becomes fertilized, since the ovary is full of spermatozoa, and thence makes its way into the uterus. This passage has not been observed.

11. The youngest uterine ovum observed has no nucleus. In one such ovum a projection containing threads of chromatin

was present on the surface of the egg, which projection may have signified the point of entrance of a spermatozoon.

12. A small spindle appears at one point at the periphery of the egg. A male pronucleus is present at the opposite side; it is very small, with a few small chromatin particles and a radiate arrangement of the protoplasm round it.

13. The spindle divides, forming a polar body, a second being subsequently formed in the same way. The process is apparently one of normal indirect nuclear division.

14. The remainder of the spindle remains in the egg as the female pronucleus. It lies a little distance from the surface, and is lobed. The male pronucleus is a large round body lying near the centre of the ovum, and in *P. capensis* is connected with the side removed from the female pronucleus by a wedge-shaped mass of protoplasm, which is denser than that of the rest of the egg.

15. The two pronuclei approach the centre and lie close together. They are both lobed (only observed in *P. Balfouri*).

16. They probably conjugate, though the process has not been observed.

17. The resulting nucleus, which is the first segmentation nucleus, passes to the periphery. It is large and lobed, and soon becomes surrounded by a large mass of dense protoplasm.

#### Summary of Events in the Maturation of the Ovum of *Peripatus Novæ-zealandiæ*.

1. The ovary resembles that of *P. capensis* in structure. Spermatozoa are present in the receptacula seminis and not in the ovary. Yolk was present in the ovary in one case.

2. The ova arise by a growth of any of the cells of the germinal epithelium. They are attached to the ovary by stalks which are formed from the cells of the germinal epithelium.

3. The nucleus of the ovum is at first coarsely granular and contains a nucleolus which is placed almost centrally.



4. The nucleus becomes vacuolate.

5. The vacuolate tissue of the nucleus passes to its border and there forms a thick wall; the centre of the nucleus in which the nucleolus lies is clear and does not stain.

6. The wall of the nucleus loses its vacuolate structure and becomes solid and homogeneous.

7. During these changes in the nucleus the ovum has increased in size, the shell has become thick, and small round, highly-refractive yolk-granules have arisen in the protoplasm of the cell.

8. The nucleus acquires an irregular outline, which is caused by peripheral portions of its substance passing out into the cell plasma, where they are visible as spheres of various sizes.

9. The whole of the nucleus with the exception of the nucleolus breaks up in this way; the spheres to which it gives rise probably become metamorphosed into yolk.

10. The protoplasm becomes vacuolate, the boundary between the egg and its follicular stalk disappears, and nuclei pass from the latter into the substance of the former. The nucleolus is not visible.

11. The follicular stalk becomes hollow, and nuclei from its walls, and yolk pass along it into the ovum from the ovary.

12. The follicular nuclei are no longer visible and probably become transformed into yolk.

13. A large nucleus appears in the ovum, lying near its point of attachment to the stalk, the boundary between the two being again established. The origin of this nucleus is not known.

14. The youngest ovum in the uterus has no nucleus visible.

15. The origin of the segmentation nucleus is unknown.

16. No polar bodies have been observed.

#### GENERAL CONSIDERATIONS.

Recently much work has been done on the subject of the origin of the ova and the phenomena of maturation and fertilization. I shall not attempt here to give a complete review

of the subject, but shall merely touch upon some observations of previous observers which seem to have a bearing on the course of events in *Peripatus*, and call attention to those points in the latter which appear to me to be of special interest.

For the sake of convenience I have arranged these points under separate headings.

The only observations which have hitherto been made on the ovarian ova of *Peripatus* are by Stuhlmann (17) on the species *P. Edwardsii*, and the account given by him is very incomplete.

#### Origin of the Ova from the Germinal Epithelium.

As I said above, the ova arise from the germinal epithelium by a process of simple growth of any of its nuclei and an aggregation of protoplasm round them. There are no cell outlines in the germinal epithelium, a condition which Stuhlmann (17) also states to exist in all the ova which he examined; and there is no distinction between such nuclei as will or will not give rise to ova.

There is no formation of nutritive and follicle cells from the germinal vesicle of the ovum such as is described by Will (19), as taking place in *Colymbetes fuscus*, or by Balbiani (1) in *Geophilus*, but the cells of the stalk and follicle are simply some of the ordinary nuclei of the germinal epithelium which have this function instead of that of becoming ova.

The germinal spot is present from the beginning in the ovum, being visible as soon as the latter begins to grow beyond the size of the ordinary nuclei of the germinal epithelium. It is always easy to distinguish it by its size from the rest of the chromatin of the germinal vesicle, and I never found more than one germinal spot. Will (19) and Scharff (13) in the ova of *Colymbetes* and osseous fishes respectively, both state that a special nucleolus or germinal spot is not present from the beginning, and hence conclude that it possesses no special morphological importance. Although it is present from the beginning in *Peripatus* I do not wish to maintain that its

presence points to its possessing any special function, since I am not able to trace any such, and it appears to be completely absorbed before the disappearance of the nucleus, and does not, as Blochmann (5) describes in *Neritina fluviatilis*, break up and give rise to the chromatin particles of the nuclear plate.

### Disappearance of the Germinal Vesicle.

The existence of a stage in the ripening of the ovum in which no nucleus is visible has now been described in almost all eggs whose maturation has been at all completely investigated. In many of these cases the mode of disappearance has not been observed, but in most of those in which the process has been seen it is similar to that which I have described in *Peripatus capensis* and *P. Balfouri*, namely, that the nucleus loses its round shape, its outline becomes irregular, and by the loss of its membrane its contents mingle with and finally become indistinguishable from the protoplasm of the egg. Between this stage and that at which the nucleus is again visible, when it is small and in the spindle stage about to bud off the second polar body, there is no trace of the germinal vesicle in the ovum. I wish here to draw attention to the fact that my observations were made on complete series of sections of well-preserved ova, so that the probability of my having overlooked it is not great. This mode of disappearance has been described by Henking (10) in *Phalangeden*, and by Stuhlmann (17) in a considerable number of insects. The loss of the nuclear membrane is also described by Scharff (13) as occurring in some osseous fishes, although he does not state that all trace of the nucleus disappears. Lankester (12) also describes a stage in the ovum of *Sepia* in which no germinal vesicle is present.

Blochmann (5) describes in *Neritina fluviatilis* the loss of the nuclear membrane, and consequent mingling of the nucleo- and egg-plasma, but states that the germinal spot remains, and, breaking up, gives rise to the chromatin of the nuclear plate. This certainly cannot be the case in the Cape

species of *Peripatus*, since the germinal spot disappears before the germinal vesicle.

Stuhlmann suggests that the disappearance may have some connection with the presence of yolk in the egg, since he has observed it in all insect eggs in which yolk is present in large quantities, but not in *Aphides* and *Cecidomya*, in which yolk is absent. Its disappearance in *Peripatus capensis*, however, in which no yolk is present, goes against this theory, unless it is to be regarded as a survival from the time when yolk was present in the ovum. On the other hand, it is supported by the observations of Will (20) and Scharff (13), who state that some of the yolk is derived from the germinal vesicle, and by the phenomena which I have described in *P. novæ-zealandiæ*; but these points will be discussed later under the Formation of the Yolk.

Stuhlmann (17) has not observed the disappearance of the germinal vesicle in *P. Edwardsii*, but this may be due to the incompleteness of his researches in this species.

The double disappearance of the germinal vesicle in *P. novæ-zealandiæ* is, so far as I know, unparalleled, and I am unable to offer any explanation of it. The first disappearance seems to be that which is homologous with that which commonly occurs in ova, and its mode of disappearance will be discussed later on. The details of the second disappearance are quite unknown, and at first sight it would appear that the nucleus shown in the ovum in fig. 30 was the first segmentation nucleus; but that this is not the case seems certain from the fact that a large proportion of the unsegmented ova which were found in the uterus were without any nucleus, and it is not easy to conclude that this condition was abnormal since the ova were found in several different parents, and were preserved in several ways. The only case in which, so far as I know, a double disappearance has been described, is that of *Millepora*, in which Mr. Hickson (11) states that the nucleus is dispersed before and after the formation of the polar bodies; but since in *P. novæ-zealandiæ* I have observed no polar bodies, it is not possible to compare the two cases.



### The Formation of the Polar Bodies.

The formation of both polar bodies takes place in the same way, and the process is evidently one of perfectly normal indirect nuclear division, there being no trace of the phenomena described by van Beneden (4) in *Ascaris megalocephala*; but it is needless to discuss these further, since they have been since contradicted by Carnoy (7). One peculiar point is the direction of the spindle, being parallel to the surface of the ovum, and not at right angles to it, the result being that the polar body does not lie immediately above but to one side of the germinal vesicle. Whether this is a point of any importance I am not able to state; but so far as I have been able to determine, its direction does not exert any influence on the subsequent history of the ovum. In all cases, as far as I know, which have been hitherto described, the spindle lies at right angles to the surface, and consequently the polar bodies lie immediately above the germinal vesicle.

That the polar bodies have all the characters of true cells I think there can be no doubt, since, as is shown in figs. 20 *a*, *b*, the first polar body is exactly similar in structure to the ovum itself, from which it differs only in size. Both its nucleus and the surrounding protoplasm possess all the characters of those of the ovum, and it is perfectly clear that not only one end of the spindle but also the protoplasm round it, are extruded in the polar body.

Contrary to the account given by Fol (8) for *Asterias glacialis*, the germinal vesicle, after budding off the first polar body, passes through a resting stage, as is shown in figs. 19 and 20 *a*, and the end of the spindle does not become transformed at once into a second spindle.

The entire absence of polar bodies in *P. novæ-zealandiæ* militates against Weismann's (18) theory as to their meaning, which is based on the hypothesis that two are found in all fertilized, and one in parthenogenetic ova. It is possible that they may have escaped my notice, but it seems hardly likely

that if they existed I should have seen no trace of them, since they were in every case very prominent objects in both the Cape species; and even if the bodies themselves had become artificially detached, the depression in which they lay would have been visible and also the stage of the nucleus preparatory to their being budded off from it. Besides, the numerous cases described by Stuhlmann (17) in which they were absent, and it is hardly possible that he could have missed them in so many cases, point to the conclusion that they are not universally present in fertilized Arthropod eggs. The two polar bodies in the Cape species are exactly similar to one another, a condition which might hardly be expected if their meanings were so different as Weismann (18) suggests.

Their presence in the Cape species and the absence in the New Zealand one suggests that they are in some way dependent on the yolk, since this is the main difference between the eggs.

### Formation of the Yolk.

The question as to the origin of the yolk has received considerable attention, and various observers have brought forward several theories as to its mode of formation. The principal of these are :

(1) That the yolk arose in the protoplasm of the egg itself. This view was upheld by Professor Balfour (2). Stuhlmann (17) states that this occurs in the Arthropod ova which he investigated.

(2) From the breaking up of the germinal vesicle. As far as I know this mode of origin has only been recently described by Will (20) and Scharff (13).

(3) From the follicle cells (inner capsule) as described by Lankester (12) in *Sepia*, by Will (20) in *Nepa*, and by Beddard (3) in *Lepidosiren*.

*P. novæ-zealandiæ* is interesting as affording an example of ova in which the yolk is formed in all these three ways, all three being very clearly seen in sections of the ova.

The yolk also arises from a fourth source, viz. from yolk

which is present in the ovary itself. This yolk is most plentiful just beneath the thin part of the ovarian wall, and is scarcer just below the germinal epithelium. It is possible that this is comparable to the condition found in Platyhelminthes, where a special part of the female organs is occupied in the formation of yolk, while in the form *Macrostomum* (2), as in *P. novæ-zealandiæ*, the function is actually performed in part of the ovarian tube itself instead of a special gland being set aside for it. I have no observations as to the origin of the small amount of yolk in the Cape species, but this is of little interest as it is obviously only a remnant of the large amount which is present in the New Zealand species.

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## EXPLANATION OF PLATES XXIX, XXX, &amp; XXXI,

Illustrating Lilian Sheldon's paper on "The Maturation of the Ovum in the Cape and New Zealand Species of *Peripatus*."

All the figures were drawn from the sections with Zeiss's camera lucida. The degree of magnification, or the powers under which they were drawn, are mentioned after the description of the figures. In those which were drawn under an immersion lens the details were examined under Powell and Lealand's apochromatic oil immersion lens n.a. 1.40, eyepieces 10 and 20.

*Alphabetical List of Reference Letters.*

*C. O.* Cavity of ovarian tubes. *Fol.* Follicle. *Fol. Nu.* Follicle nuclei. *G. Ep.* Germinal epithelium. *G. S.* Germinal spot. *G. V.* Germinal vesicle. *I. Ep.* Epithelium lining ovary. *Nl.* Nucleolus. *Nu.* Nucleus. *O. Ep.* Outer epithelium of ovary. *O. S.* Egg-shell. *Ov.* Ovum. *P. b. 1.* First polar body. *P. b. 2.* Second polar body. *Ped.* Peduncle attaching ovum to ovary. *Per.* Wall of pericardium. *Pron. ♂.* Male pronucleus. *Pron. ♀.* Female pronucleus. *Sp.* Spermatozoa.

FIG. 1.—Transverse section of the ovarian tubes of *Peripatus capensis* at the end of April, after the ova have passed into the uterus. *C. O.* Cavity of ovarian tube. *G. Ep.* Germinal epithelium. *Per.* Wall of pericardium. *Sp.* Spermatozoa. Zeiss, oc. 2, obj. B.

FIG. 2.—Section of a small portion of the wall of the ovarian tube of *P. capensis* at the end of April, highly magnified. *I. Ep.* Epithelium lining the cavity. *O. Ep.* Outer epithelium. Zeiss, oc. 2, Reichert's  $\frac{1}{15}$ th oil imm.

FIG. 3.—Section of a portion of the germinal epithelium of *P. capensis* in July. *C. O.* Cavity of ovarian tube containing spermatozoa. *G. S.* Germinal spot. *G. V.* Germinal vesicle. *Ov.* Ovum. Zeiss, oc. 3, obj. C C.

FIG. 4.—Section of a portion of the germinal epithelium of *P. capensis* in September. Letters as in Fig. 3. Zeiss, oc. 3, obj. C C.

FIG. 5.—An ovum and its attachment, from the same ovary as Fig. 4. *G. S.* Germinal spot. *G. V.* Germinal vesicle. *O. S.* Egg-shell.

FIG. 6.—Nucleus of an ovarian ovum of *P. capensis* shortly before its disappearance, showing its crinkled outline. Greatest length of nucleus .045 mm. *Nu.* Nucleus. *O. S.* Egg-shell. Zeiss, oc. 2, Reichert's  $\frac{1}{15}$ th oil imm.

FIG. 7.—Last stage of the nucleus in *P. Balfouri* before its complete disappearance: Zeiss, oc. 2, Reichert's  $\frac{1}{15}$ th oil imm.

FIG. 8.—Two ovarian ova of *P. capensis* of April; in one the nucleus and nucleolus are still present, in the other both have disappeared, and the ovum lies loose in its follicle. *Fol.* Follicle. *Nl.* Nucleolus. *Nu.* Nucleus. *O. S.* Egg-shell. *Ped.* Peduncle.

FIG. 9.—Ovarian ovum of April of *P. capensis* shortly before the nucleus disappears, showing its peduncle and follicle. *Fol.* Follicle. *Nu.* Nucleus. *O. S.* Egg-shell. *Ped.* Peduncle. Magnified 600 diameters.

FIG. 10.—Ovum of *P. capensis* shortly after it has passed into the uterus; the nucleus is absent; a small prominence on the surface is present, which may be the point of entrance of the spermatozoon. Magnified 600 diameters.

FIG. 11.—Section of an ovum of *P. capensis*. The male pronucleus is just formed; the nucleus is in the spindle stage, preparatory to budding off the first polar body. *Pron.* ♂. Male pronucleus. *Nu.* Nucleus. Magnified 600 diameters.

FIG. 12.—Ovum of *P. capensis*, in which the nucleus is again present after its disappearance in spindle form. The spindle is seen in transverse section. Magnified 600 diameters.

FIG. 13.—Ovum of *P. capensis*, in which the nucleus is in the spindle stage after budding off the first polar body. *Nu.* Nucleus. *P. b. 1.* First polar body. Magnified 600 diameters.

FIG. 14 *a* and *b*.—Two sections through an ovum of *P. capensis*.

Fig. 14 *a* shows the nucleus and the second polar body, which has just been budded off.

Fig. 14 *b* shows the male pronucleus lying in the centre of the ovum. The sections from which the two figures are drawn are separated by twelve intervening ones. *P. b. 2.* Second polar body. *Pron.* ♂. Male pronucleus. *Nu.* Nucleus. Magnified 600 diameters.

FIGS. 15—20.—Consecutive stages, showing the changes undergone by the nucleus in the formation of the polar bodies. Zeiss, oc. 2, Reichert's  $\frac{1}{15}$ th oil. imm.

Fig. 15. The nucleus in spindle stage, before the formation of the first polar body. The chromatin forms an equatorial plate.

Fig. 16. The equatorial plate is divided into two bands. (This is in the formation of the second polar body.)

Fig. 17. The chromatin bands are completely separated, and are approaching the ends of the spindle. (From P. Balfouri.)

Fig. 18. The chromatin lies at the ends of the spindle-fibres.

Fig. 19. The first polar body is just separating from the ovum, the spindle-fibres are still visible in the polar body. *P. b. 1.* First polar body.

Fig. 20 *a* and *b*. Two sections slightly removed from one another, showing the resting condition of the nucleus after the formation of the

first polar body. The histological characters of the polar body (Fig. 20 *b*) are precisely similar to those of the nucleus and its surrounding protoplasm.

FIG. 21.—Male pronucleus of *P. Balfouri* shortly after its formation. *Pron.* ♂. Male pronucleus. Zeiss, oc. 3, Reichert's  $\frac{1}{15}$ th oil imm.

FIG. 22.—Transverse section through one half of the ovary of *P. Balfouri* in December. *C. O.* Cavity of ovarian tube. *Fol.* Follicle. *G. S.* Germinal spot. *G. V.* Germinal vesicle. *Ov.* Ovum. Zeiss, oc. 3, obj. C C.

FIG. 23.—Ovum of *P. Balfouri* of April, while the nucleus is still in the centre. Letters as in Fig. 22. Magnified 600 diameters.

FIG. 24.—Ovarian ovum of *P. Balfouri* after the disappearance of the nucleus. Magnified 600 diameters.

FIG. 25.—Ovum of *P. Balfouri*, in which the male and female pronuclei lie close together and are apparently about to conjugate. Magnified 600 diameters.

N.B.—The remaining figures are of *P. novæ-zealandiæ*; in them the yolk is coloured yellow.

FIG. 26.—Transverse section of the ovary of *P. novæ-zealandiæ*. *C. O.* Cavity of ovarian tube. *Ov.* Ovum. *Per.* Wall of pericardium. Zeiss, oc. 3, obj. A.

FIG. 27.—Ovum of *P. novæ-zealandiæ*, in which the germinal vesicle is central and has a homogeneous regular wall. *Fol.* Follicle. *G. S.* Germinal spot. *G. V.* Germinal vesicle. *O. S.* Eggshell.

FIG. 28.—Ovum of *P. novæ-zealandiæ*, in which the germinal vesicle has a crinkled outline. Letters as in last figure.

FIG. 29.—Ovum in which the germinal vesicle has broken down.

FIG. 30.—Ovum with large excentric nucleus and great mass of yolk, from a December ovary.

FIG. 31.—Ovum in which the germinal vesicle is absent, showing the passage into the ovum of nuclei of the follicle. *Fol.* Follicle. *Fol. Nu.* Nuclei from the follicle in substance of ovum. *Ov.* Ovum.

FIG. 32.—Ovum in which the peduncle has become hollow, and yolk appears to be passing down it from the cavity of the ovarian tubes.





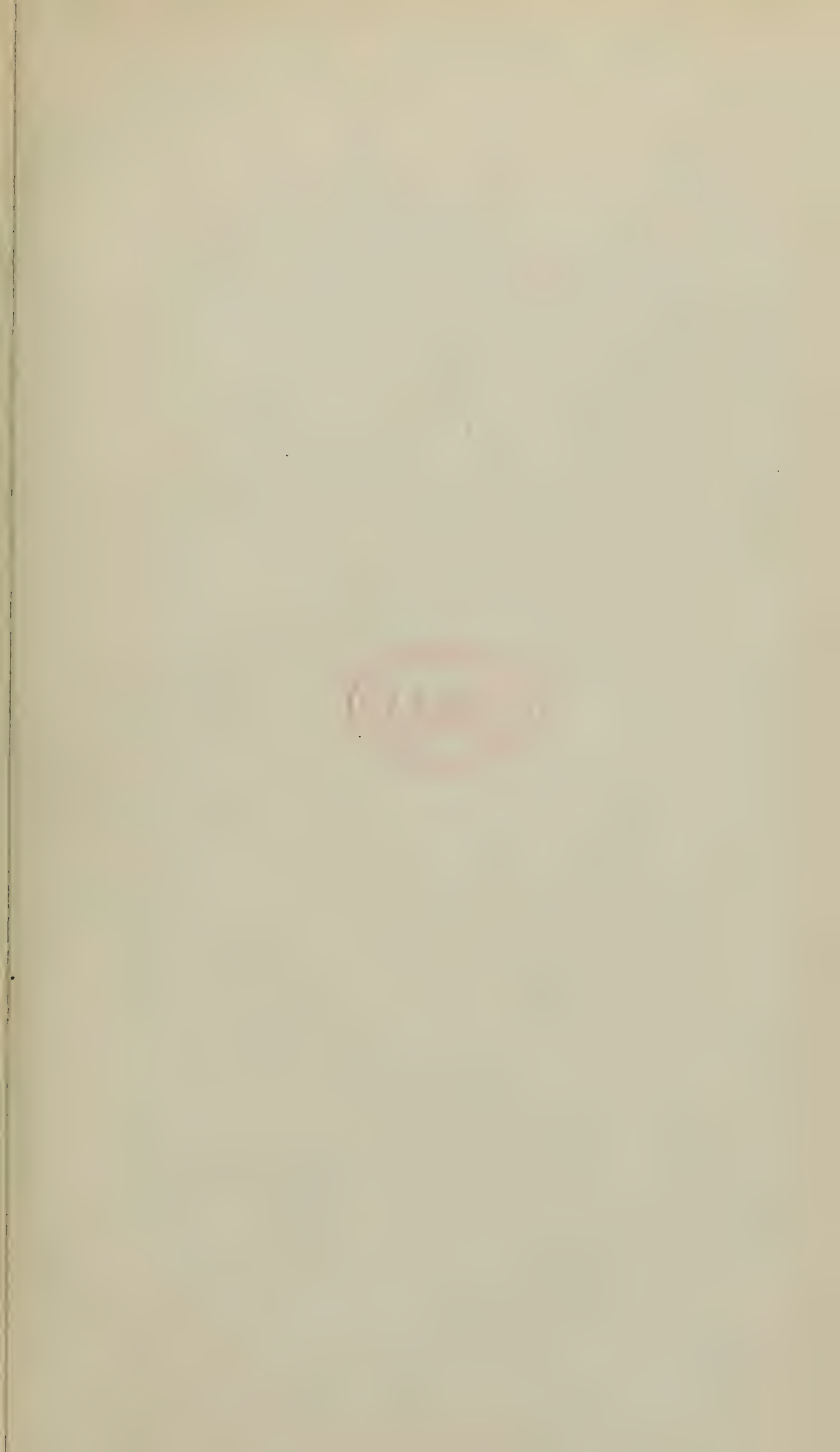


Fig. 1.



Fig. 3.

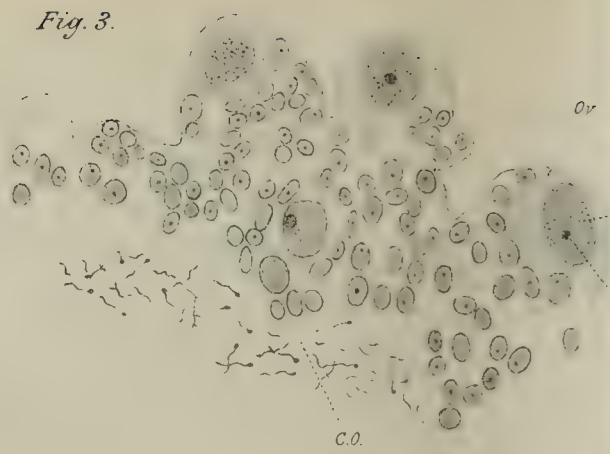


Fig. 2.

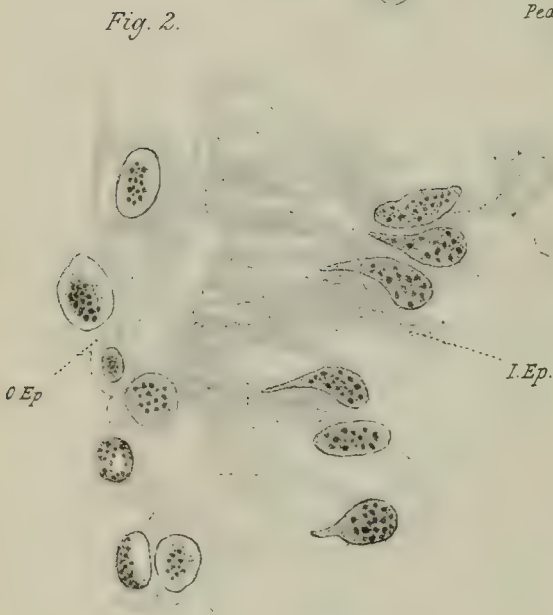


Fig. 8.



Fig. 6.

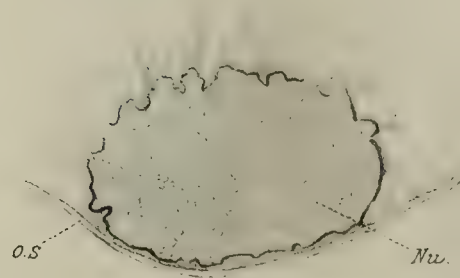


Fig. 7.

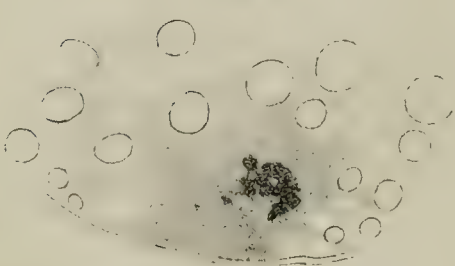


Fig. 4.



Fig. 5.



Pron ♂

Fig. II.

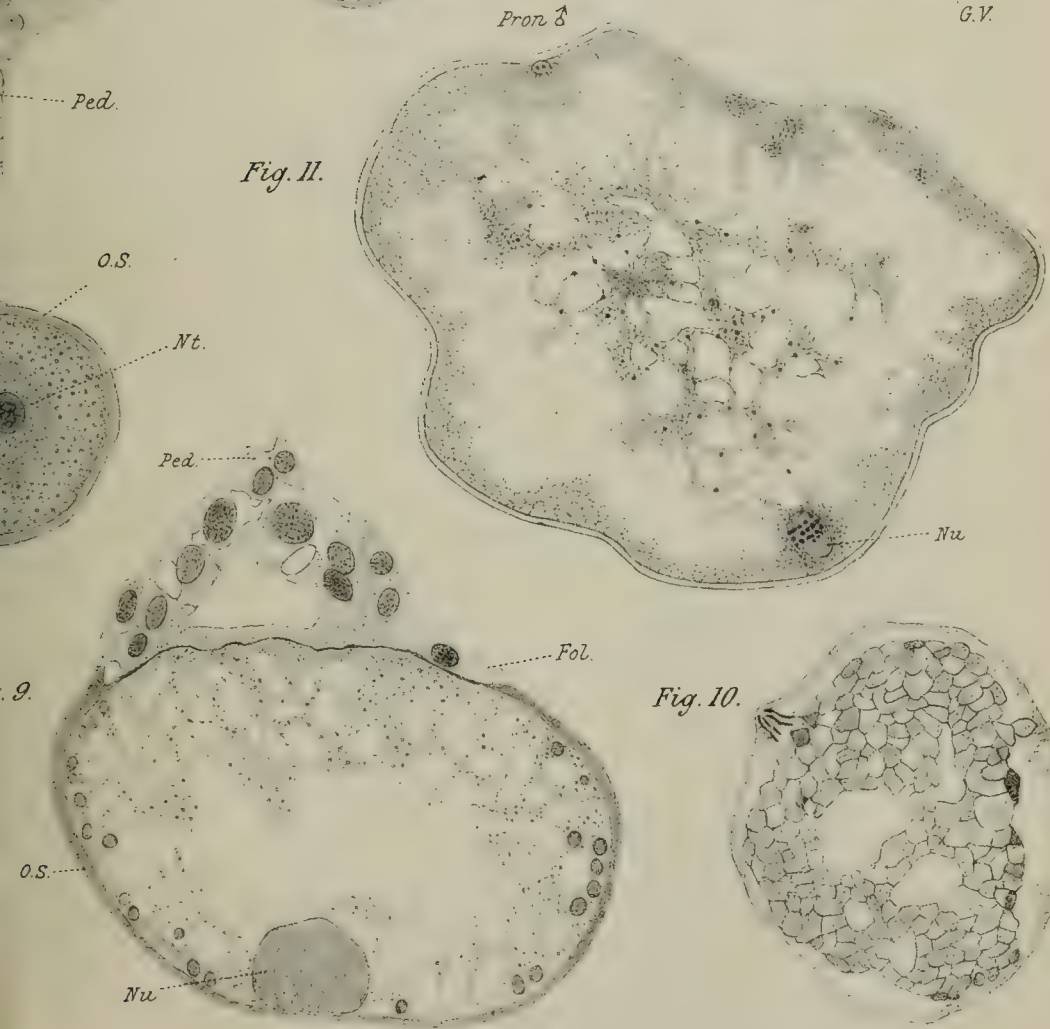
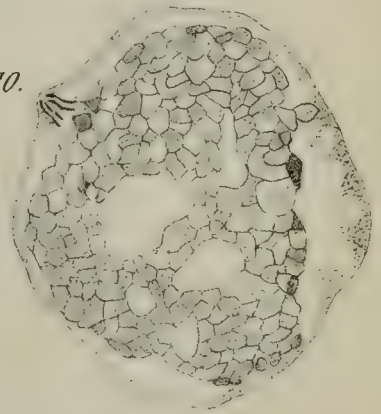


Fig. 10.







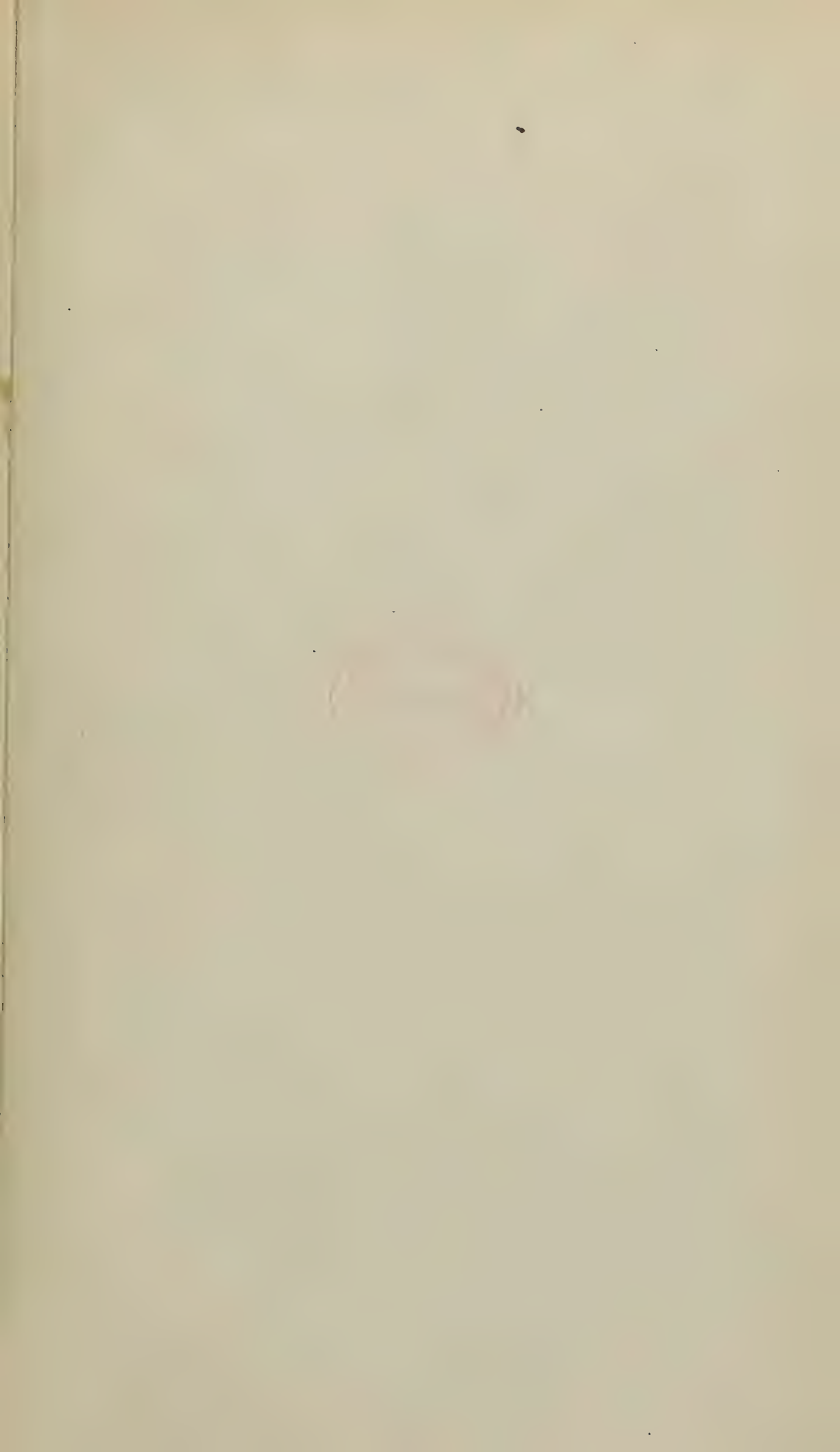


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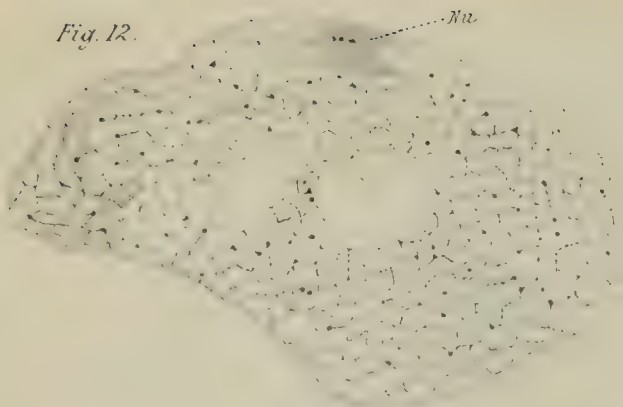


Fig. 13.

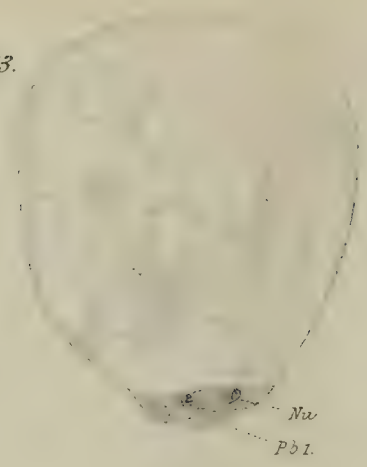


Fig. 14.

Fig. 16.

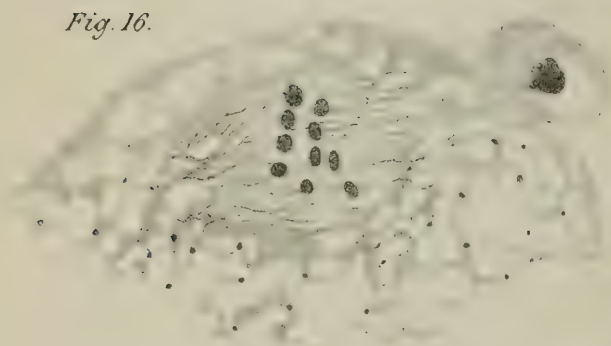


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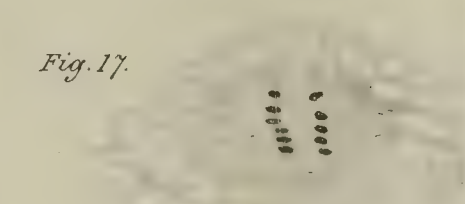


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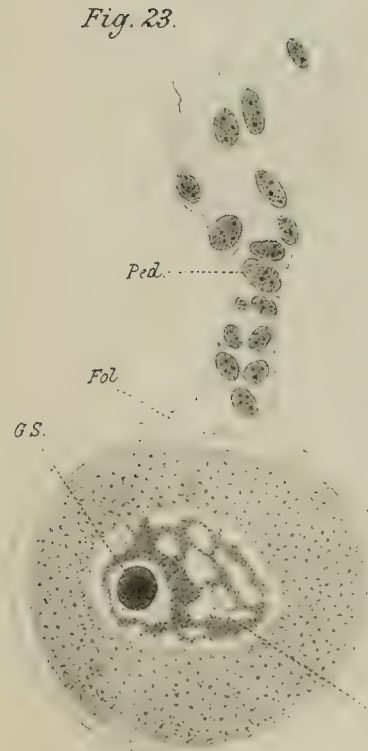
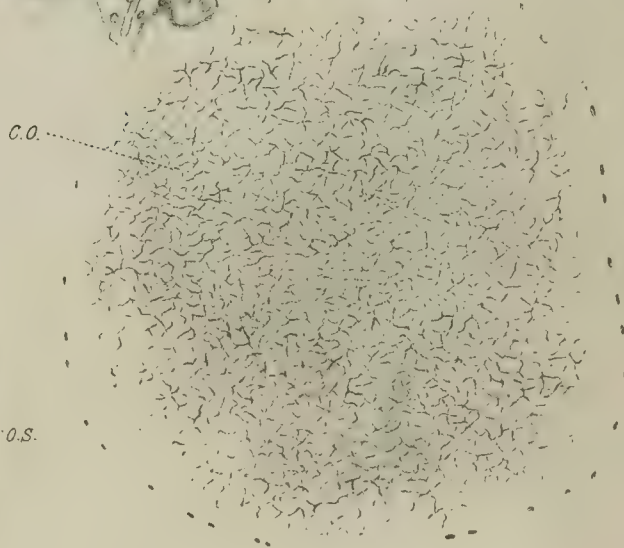


Fig. 22.



Fig. 25.



Pro

Fig. 14 b.

Fig. 15.

Pron. ♂

Fig. 19.

Pb. 1.

Fig. 18.

Pb. 1.

Fig. 20 b.

Fig. 20 a

Nu

Fig. 21.

Pron. ♂

Fig. 24.

Fig. 26.

Per.

C.O.

OV.

OV.

Pron. ♀





Fig. 27.

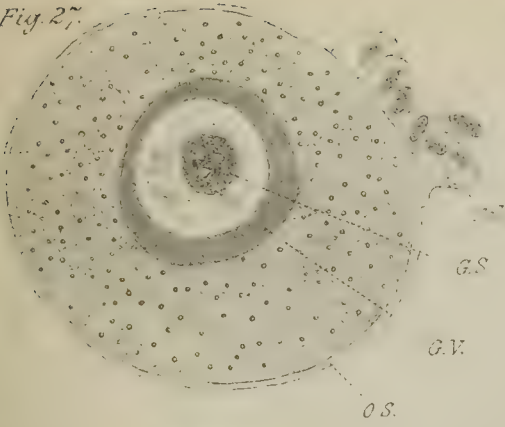


Fig. 28.

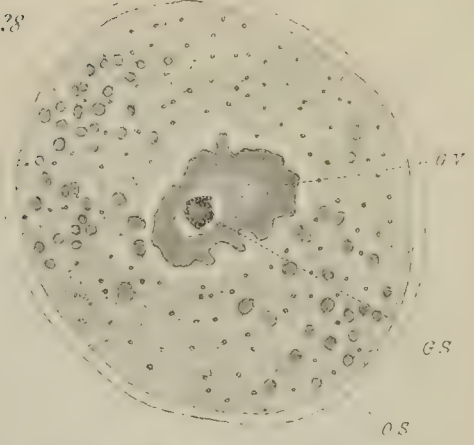


Fig. 30.

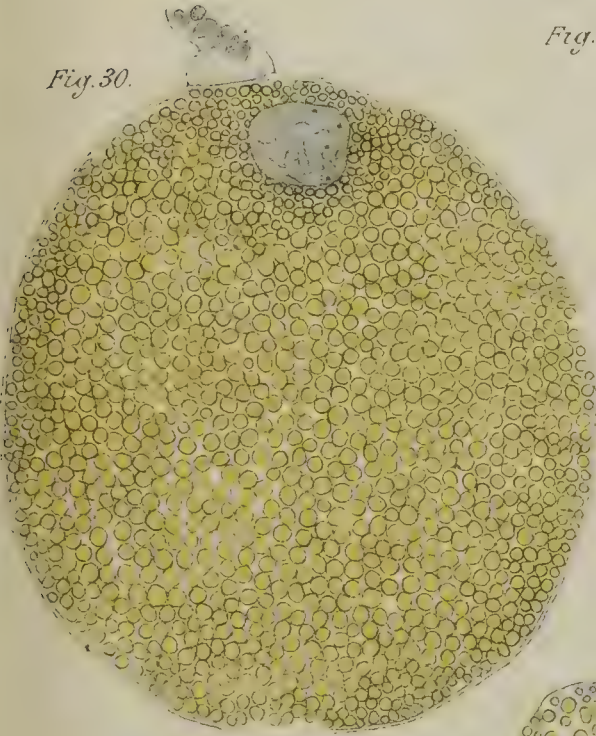


Fig. 29.



Fig. 32.

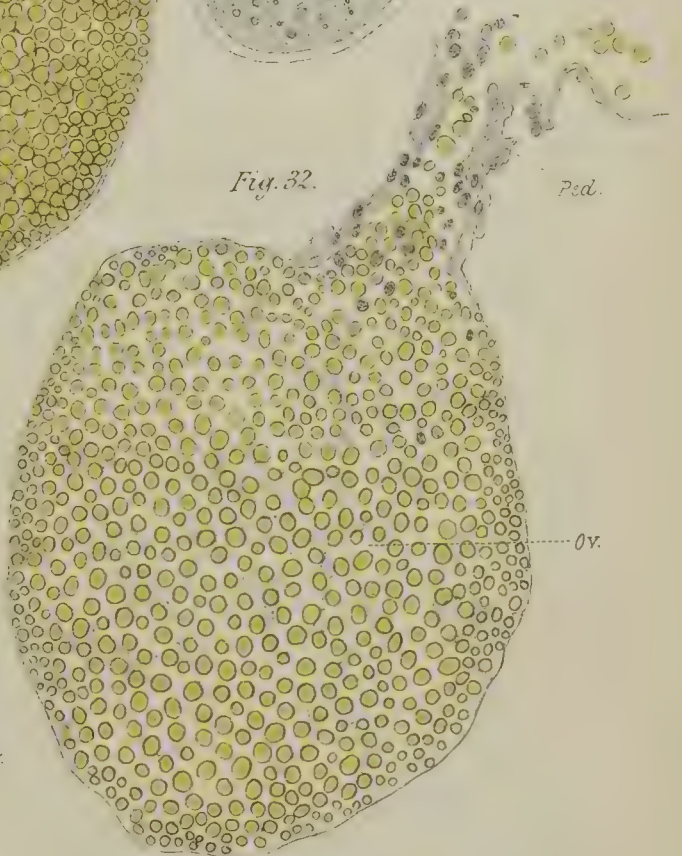
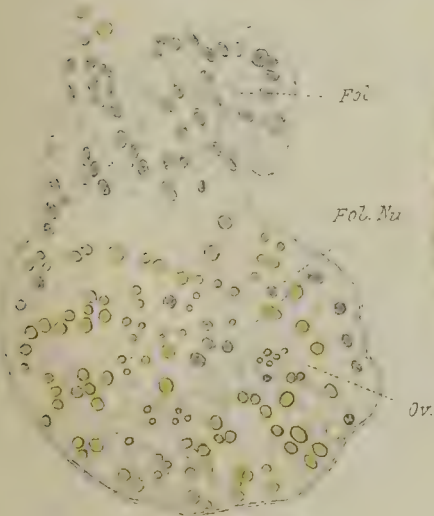


Fig. 31.





NOTES ON THE ANATOMY OF PERIPATUS  
CAPENSIS AND PERIPATUS NOVAE-  
ZEALANDIAE.

BY

LILIAN SHELDON,

Bathurst Student, Newnham College, Cambridge.

THERE are a few anatomical details in which these two species of *Peripatus* differ both from one another and from *P. Edwardsii*, the anatomy of which has been described by Gaffron (2).

CRURAL GLANDS.

I have examined several legs of *P. capensis*, both of males and females, and have found a crural gland in every one, except the first pair of legs.

Except those of the fourth and fifth, and in the male of the last pair of legs, the glands all resemble one another in their structure, in the position of the gland and duct, and in the point at which the latter opens, viz. on the ventral surface of the leg external to the opening of the duct of the segmental organ.

The glands of the fourth and fifth pairs of legs are very much smaller than the others, and open internally to the segmental organs, in the angle formed by the junction of the leg with the body. The gland of the last leg of the male is very long, and extends forwards through many segments of

the body, being apparently modified in connection with the male generative organs.

These organs have all been previously described by Professor Balfour (1).

In none of the legs of *Peripatus novae zealandiae*, of which I examined sections, did I find any crural glands, either in the male or female. I took legs from the various parts of the body in both sexes, and in all cases the segmental organs were present, and the legs contained a much larger supply of muscles than those of *P. capensis*, but there were no traces of crural glands in any case, even in the last leg of the male.

In *P. Edwardiis* Gaffron (2) states that the crural glands are absent in the female, but are present in some of the segments of the male, there being in some of them two pairs.

#### SEGMENTAL ORGANS.

In *Peripatus novae zealandiae* the external aperture of the generative apparatus is placed on the ventral surface of the body in front of the last (fifteenth) pair of legs. In this pair of legs there are no segmental organs, so that the generative ducts are apparently the modified segmental organs of the last segment.

In *Peripatus capensis*, in which the generative aperture is situated at the posterior end of the body, immediately in front of the anus and behind the last pair of legs, segmental organs are present in the latter.

In *P. novae zealandiae*, as was described in *P. capensis* by Professor Balfour (1), the segmental organs of the fourth and fifth pair of legs are much larger than the rest.

#### ACCESSORY GLANDS OF THE MALE.

In *P. capensis*, in addition to the enlarged crural glands of the last pair of legs, the male generative apparatus is provided with a pair of glandular tubes, which lie on each



side, and dorsally to the ductus ejaculatorius, into which they open at the point where it opens to the exterior. These accessory glands were first mentioned by Professor Moseley (4), and their position and mode of opening were described by Professor Balfour (1).

In *P. novae zealandiae* these accessory glandular tubes are also present, but their relations are somewhat different. They lie more laterally in the body. Each gland starts as a blindly-ending tube near the posterior end of the body, and passes forwards for a short distance. It then bends sharply on itself, and passes backwards to its external opening, which is situated near the posterior end of the body at its ventro-lateral angle, external to the nerve-cord. This position of their openings is clearly seen, both on dissection and in sections. Thus they open quite independently of the vas deferens, therein differing from those of *P. capensis*. They also differ from the accessory glands of *P. Edwardsii*, which Gaffron (2) describes as opening with the anus.

#### VAS DEFERENS.

To the naked eye the main difference between the vas deferens of *P. capensis* and that of *P. novae zealandiae* appears to be in their relative lengths, that of the former being much the shorter. This difference seems to be due to the very great difference between the spermatophores formed by the two species.

The vas deferens of *P. novae zealandiae* very closely resembles that described by Gaffron in *P. Edwardsii*. The whole of the posterior part of the duct is filled by an enormously long spermatophore, which is surrounded by a horny case. The internal cavity is enlarged in several places and in these regions is filled with spermatozoa, the external case being thin and composed of a single layer. In the remainder of the spermatophore the lumen is very small, and the case very thick and composed of several layers of horny substance. The whole

spermatophore has, in fact, precisely the same structure as that described by Gaffron in *P. Edwardsii*.

The structure of the walls of the vas deferens of *P. novae zealandiae* is also similar to that of *P. Edwardsii*, except that the secretion globules are arranged in irregular masses in the cells near their ends, which abut upon the lumen, instead of having the regular arrangement described as occurring in the latter. The structure of the walls of the testes in *P. novae zealandiae* differs from that of *P. Edwardsii*, in that in the latter Gaffron (2) states that there is no epithelial lining, whereas those of the former are lined by a layer of fairly deep columnar cells with large nuclei, their ends, which abut upon the lumen, being rounded. There is a layer of muscles external to the epithelium.

In *P. capensis* the spermatophores are small rounded bodies, enclosed in a thin, structureless case, and filled with spermatozoa.

In its lower part, where the vas deferens is filled with spermatophores, the cells lining it are somewhat flat, are much vacuolated, and stain very slightly. Just in front of the region where the fully formed spermatophores lie the cells are continued into small masses of unstained matter containing very deeply staining globules lying in the lumen of the duct. These masses probably form the cases of the spermatophores, and are secreted by the cells with which they are continuous. In front of this region the cells become columnar, the nuclei being closely packed at the bases of the cells. The cell protoplasm also stains very deeply. The spermatophores of *P. capensis*, after they have been shed, are easily seen by examining with a lens the dorsal surface of a female. They appear as small, round, whitish bodies, lying on the skin of the animal, and when teased are found to be filled with spermatozoa.

I have not had the good fortune to see a spermatophore of *P. novae zealandiae* after it has been shed, and I only assume that the horny case found in the vas deferens is a spermatophore, because Professor Moseley (4) and Gaffron (2) both describe it

as such. But it is strange that it should differ so largely from *P. capensis* in this respect.

The ovarian funnel (receptaculum ovarum of Kennel (3)), described by Gaffron (2) in *P. Edwardsii* as lying on the oviduct, between the ovary and the receptaculum seminis, is not present in *P. novae zealandiae*. The receptaculum seminis, with its two ducts, is present, and the oviduct in that region is much coiled and vesiculated.

These observations were made at the suggestion of Mr Sedgwick, to whom I am indebted for providing me with the necessary material.

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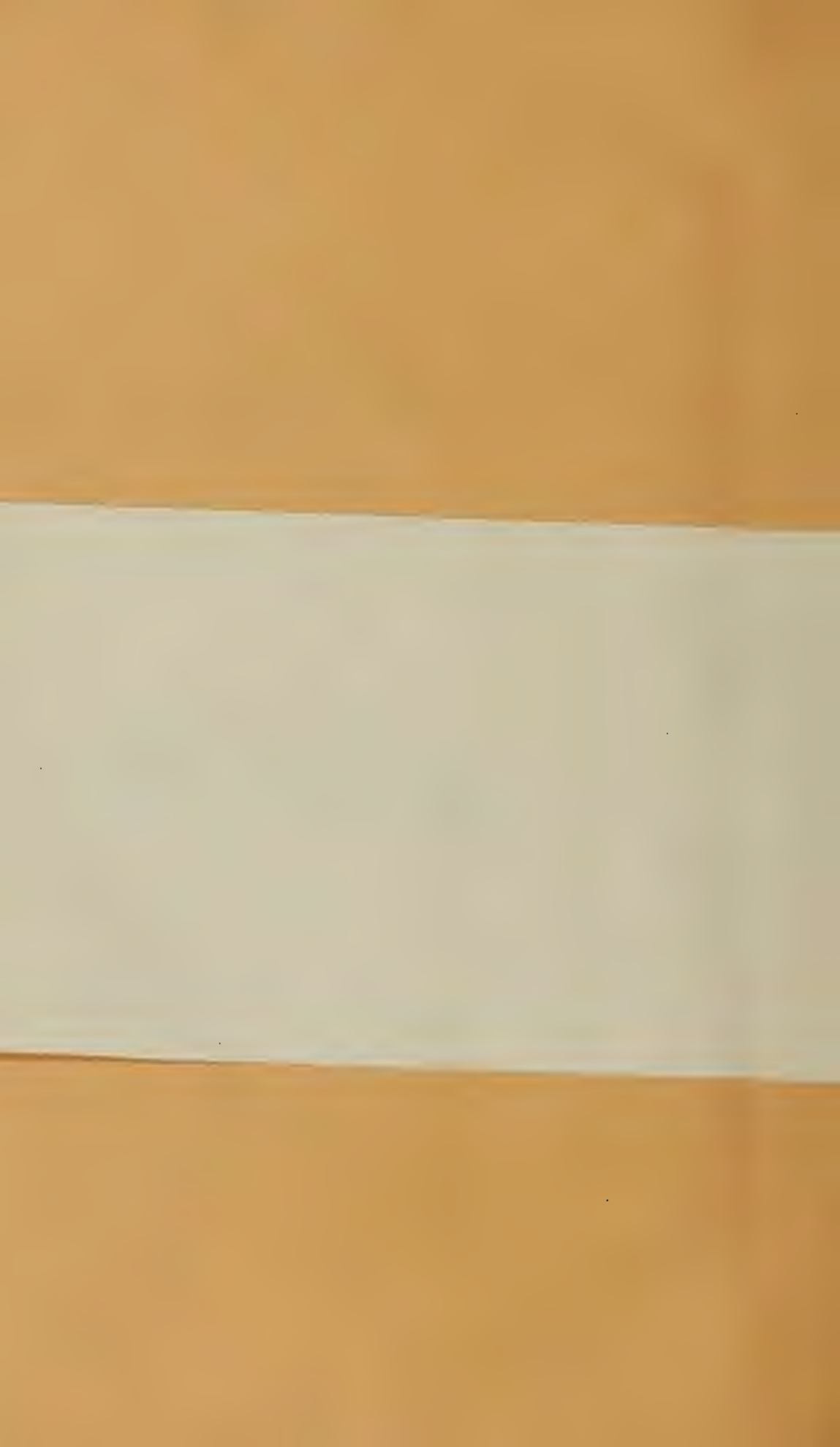
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